

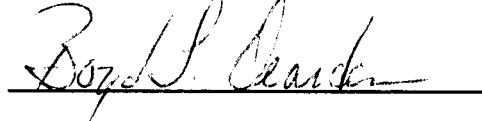
To the Graduate Council:

I am submitting herewith a thesis written by Katie Greenberg entitled "Gray Fox Ecology in East Tennessee: Food Habits, Home Range, and Habitat Use." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.


Michael R. Pelton, Major Professor

We have read this thesis
and recommend its acceptance:





Accepted for the Council:


Vice Provost
and Dean of The Graduate School

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a Master's degree at The University of Tennessee, Knoxville, I agree that the Library shall make it available to borrowers under rules of the Library. Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgment of the source is made.

Permission for extensive quotation from or reproduction of this thesis may be granted by my major professor or, in his absence, by the Head of Interlibrary Services when, in the opinion of either, the proposed use of the material is for scholarly purposes. Any copying or use of the material in this thesis for financial gain shall not be allowed without my written permission.

Signature

Kathie Yuenberg

Date

3/14/88

GRAY FOX ECOLOGY IN EAST TENNESSEE:
FOOD HABITS, HOME RANGE, AND HABITAT USE

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee

Katie Greenberg

June 1988

ACKNOWLEDGEMENTS

Research was sponsored by the Oak Ridge National Environmental Research Park (NERP), Office of Health and Environmental Research, U.S. Department of Energy, under contract no. DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. National Laboratory.

I would like to express my sincere appreciation to my major professor, Dr. Michael Pelton, and committee members, Drs. Boyd Dearden, John Gittleman and Arthur Echternacht for their assistance and advice. Special thanks also to Patricia D. Parr, NERP manager, for her time, effort and assistance.

I also extend many thanks to Mr. H.A. Longmire for teaching me the "tricks of the trapping trade", and for his assistance; Dr. T. Fendley, Clemson University, SC, for his time and advice on this project; Lynn Snyder for identifying bone and bone fragment in gray fox scats; TWRA officer Jim Evans for his encouragement, advice and assistance; Dr. John New, University of Tennessee Veterinarian School, for his advice on anaesthetic dosage, and for providing the necessary drugs and hypodermic needles; Drs. Paul and Hazel Delcourt, Department of Botany, and Dr. P.L. Lambden, Department of Entomology and Plant Pathology for their consultation; John Schneider for his immense assistance with computer data analysis, Kathy Boyle for permitting the use of her computer program, and for her advice, and Michael O'Neil for his assistance with computer statistical procedure.

Immense thanks are due to field workers Wendy Sera, Matthew Hutchinson, Laura Stine and Vivian Brown for their assistance in the small mammal survey, and Steve Whitlock for his assistance in radio-tracking 2 coyotes. Thanks also to Tommy R. Smith for his valuable instruction on radio-telemetry technique.

Special love to my mother, my five wonderful sisters, my father, Wanda Reif, Athena "Pusti" Semitekolos and all my friends who offered love, enthusiasm and support from far away.

Finally, thanks to Stanley H. Crownover for his love and encouragement.

ABSTRACT

Examination of 170 gray fox (Urocyon cinereoargenteus) scats collected between Sept. 1986 and Aug. 1987 on the Oak Ridge Reservation (ORR), east Tennessee, revealed that plant foods were utilized most heavily, followed by invertebrate and animal prey. Proportions of the 3 categories utilized were not evenly distributed among months and were dictated by availability. Biological seasons were delineated by detection of statistically significant shifts in diet among the 3 food categories. Animal prey, predominantly rabbits and rodents, comprised 67.0% of winter (Jan.-Apr.) dry weight (100% occurrence); arthropods, predominantly 17-year locusts (Magicalicada sp.), comprised 96.1% of spring (May) dry weight (275% occurrence); plant material, predominantly persimmon, cherry, blackberry and squaw-root, comprised 92.9% of summer-fall (June-Dec.) dry weight (161.6% occurrence). This study indicated that gray foxes may switch dietary trophic level depending on seasonal food availability.

Home range sizes of gray foxes were determined from radio-telemetry data (Sept. 1986-Aug. 1987) at the ORR, East Tennessee. Minimum density was estimated at 0.45 adult gray foxes per km². Average composite home range size was 3.97 km² for 10 gray foxes, (4.41 km² for adults (n=6) and 3.32 km² for subadults (n=4)). No significant differences were detected among home range sizes between males and females or between adult and subadult foxes. Seasonal home range sizes were tested for differences based on seasons of high (spring-fall: insect and fruit prey) or low (winter: animal prey) food availability

and breeding-cycle (breeding, pup-rearing and prebreeding). Statistical analysis detected no significant differences among seasons, probably due to high variability between individual foxes. Changes in home range size among seasons for individual foxes did not correspond to any obvious pattern or environmental influence. Territoriality and monogamy were suggested by closely coinciding home ranges of adult male and female pairs, with little overlap between adult males or adult females. Extensive overlap of home ranges by subadult foxes (female, in this case) with one adult male fox indicated that family aggregations may occupy the same home range. Despite seasonally differential area-utilization, boundaries for composite home ranges seemed to be recognized by neighboring foxes year-round; "core areas" within home ranges remained relatively constant. Territoriality may be advantageous where periods of food scarcity (e.g. winter) occur. It is suggested that territory sizes are adjusted to contain a sufficient year-round food supply. All statements regarding the relationship between resource dispersion, home range size or territoriality are tentative, however, due to high variation among individuals and small sample size.

Gray fox activity patterns and habitat use also were determined from radio-telemetry data. Foxes were generally active nocturnally (66.6% active), inactive diurnally (21.9% active), and less active during early morning (26.6% active) than evening (54.3% active). Chi-square tests were used to compare activity patterns for 4 different sets of months ("seasons") based on food-type exploitation, relative food abundance, breeding cycle and degree of vegetative (foliage) cover. The most highly significant difference was detected between months of

high vegetative cover (May-Oct.), when early morning and daylight activity levels were higher, and months of low (Nov.-Apr.) vegetative cover.

A prey base study indicated (although not statistically significant) that winter small mammal populations were most abundant in mature pine habitat, followed by oldfield, deciduous forest, and young pine habitat, respectively; variation in trapping success among seasons and replicate grids, however, was high. Habitat utilization analysis showed that annually, foxes selected young pine more than expected relative to availability. Seasonal analysis based on food-type exploitation revealed that nocturnally, all habitat types were used in proportion to availability in winter and spring. In summer-fall young pine was used significantly more than expected; this may have been due to high concentrations of blackberries (which ripen in summer) within this habitat type. A slightly higher selection of mature pine was observed in winter, and might be attributed to a higher concentration of small mammals (a winter food source) within this habitat type. High daytime use of young pine habitat persisted year-round. Observed daytime resting sites were in thick early-successional vegetation, rocky ledges or underground holes. Maternal dens were dug into the roots of windthrown trees.

Hence, while changes in seasonal prey dispersion (animal, insect, and fruit prey) may not influence seasonal home range sizes, shifts in habitat use within a constant territory may occur according to location of seasonally available foods.

TABLE OF CONTENTS

PART	PAGE
I. INTRODUCTION	1
Literature Cited	6
II. GRAY FOX FOOD HABITS	8
Abstract	8
Introduction	8
Study Area	12
Methods and Materials	13
Results and Discussion	15
Summary and Conclusions	27
Literature Cited	29
III. GRAY FOX HOME RANGE, DENSITY, AND TERRITORIALITY	31
Abstract	31
Introduction	32
Study Area	41
Methods and Materials	42
Trapping	42
Radio Telemetry	43
Data Analysis	44
Results and Discussion	48
Trapping	48
Home Range and Territoriality	48
Density and Mortality	78
Summary and Conclusions	79
Literature Cited	83
IV. GRAY FOX ACTIVITY PATTERNS AND HABITAT USE	88
Abstract	88
Introduction	89
Study Area	94
Methods and Materials	95
Trapping	95
Radio Telemetry	96
Data Analysis: Activity	97
Small Mammal Sampling	98
Data Analysis: Habitat Utilization	99
Results and Discussion	102
Trapping	102
Activity	102
Relative Abundance of Small Mammals	108
Habitat Utilization	112
Daytime Resting Sites and Dens	122
Summary and Conclusions	124
Literature Cited	127

PART	PAGE
V. SUMMARY AND DISCUSSION	130
Literature Cited	137
APPENDIX	139
VITA	158

LIST OF TABLES

TABLE	PAGE
II-1. Percent frequency, number, and percent dry weight of food categories and major food items, with taxa "nested" in preceding category or class, on an annual basis, found in 170 fox scats on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	17
IV-1. Activity patterns, on an annual and seasonal basis, for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	105
IV-2. Diurnal habitat affinity index values for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987. Index values of 1.0 indicate use of that habitat in proportion to its availability; greater than 1.0 indicates higher use, and less than 1.0 indicates lower use than expected if animals utilized habitat types randomly.	114
IV-3. Nocturnal habitat affinity index values for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987. Index values of 1.0 indicate use of that habitat in proportion to its availability; greater than 1.0 indicates higher use, and less than 1.0 indicates lower use than expected if animals utilized habitat types randomly.	115
IV-4. Diurnal and nocturnal habitat utilization, on an annual and seasonal basis, for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	116
A-1. Percent frequency, number, and percent dry weight of food categories and food items, on an annual basis, with taxa "nested" in preceding category or class, found in 170 fox scats on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	140

TABLE	PAGE
A-2. Winter (January-April), spring (May), and summer-fall (June-December) comparison of percent frequency and percent dry weight of food categories and food items, with taxa "nested" in preceding category or class, found in 170 fox scats on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	144
A-3. Physical measurements of the gray foxes captured on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	150
A-4. Composite minimum convex polygon home range estimates for 5 male and 7 female gray foxes radio-tracked September 1986-August 1987, Oak Ridge Reservation, east Tennessee.	151
A-5. Minimum convex polygon home range estimates for breeding, pup-rearing, and prebreeding seasons for 5 male and 7 female gray foxes radio-tracked September 1986-August 1987, Oak Ridge Reservation, east Tennessee.	152
A-6. Minimum convex polygon home range estimates for "abundant" and "scarce" food seasons for 5 male and 7 female gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	153
A-7. Total small mammal captures and recaptures (in parentheses) in 4 habitat types over 4 seasons, September 1986-August 1987 on the Oak Ridge Reservation, east Tennessee.	154
A-8. Relative abundance and species composition (recaptures in parentheses) of small mammals between 4 habitat types on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	155
A-9. Characteristics of 16 gray fox daytime resting sites and dens on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	156

LIST OF FIGURES

FIGURE	PAGE
II-1. Mean monthly dry weights of animal, plant, and insect material in gray fox scats, Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	20
II-2. Winter (n=42), spring (n=16), and summer-fall (n=112) comparison of percent dry weight of plant, insect, and animal material in gray fox scats, Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	22
III-1. Composite home ranges of 5 adult male, 2 adult and 5 subadult female gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	50
III-2. Composite home ranges of 2 adult and 5 subadult female gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986- August 1987.	51
III-3. Composite home ranges of 5 adult male gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986- August 1987.	52
III-4. Seasonal home range areas and "core area" (darkest shading) for adult male fox 69 based on breeding (Jan.-Mar.), pup-rearing (Apr.- July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	54
III-5. Seasonal home range areas and "core area" (darkest shading) for adult male fox 76 based on breeding (Jan.-Mar.), pup-rearing (Apr.- July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	55

FIGURE	PAGE
III-6. Seasonal home range areas and "core area" (darkest shading) for adult male fox 82 based on breeding (Jan.-Mar.), pup-rearing (Apr.- July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	56
III-7. Seasonal home range areas and "core area" (darkest shading) for adult male fox 84 based on breeding (Jan.-Mar.) and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	57
III-8. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 64 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	58
III-9. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 66 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	59
III-10. Seasonal home range areas and "core area" (darkest shading) for adult female fox 74 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	60
III-11. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 78 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	61
III-12. Seasonal home range areas and "core area" (darkest shading) for adult male fox 69 based on "abundant" (May-Dec.) and "scarce" (Jan.- Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	65

FIGURE	PAGE
III-13. Seasonal home range areas and "core area" (darkest shading) for adult male fox 76 based on "abundant" (May-Dec.) and "scarce" (Jan.- Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	66
III-14. Seasonal home range areas and "core area" (darkest shading) for adult male fox 82 based on "abundant" (May-Dec.) and "scarce" (Jan.- Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	67
III-15. Seasonal home range areas and "core area" (darkest shading) for adult male fox 84 based on "abundant" (May-Dec.) and "scarce" (Jan.- Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	68
III-16. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 64 based on "abundant" (May-Dec.) and "scarce" (Jan.- Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	69
III-17. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 66 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	70
III-18. Seasonal home range areas and "core area" (darkest shading) for adult female fox 74 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	71
III-19. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 78 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	72

FIGURE	PAGE
IV-1. Annual percent activity recorded for radio-telemetry locations during sunrise, daylight, sunset and night time periods for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	103
IV-2. Percent activity recorded for radio-telemetry locations during seasons of high (May-Oct.) and low (Nov.-April) vegetative cover during sunrise, daylight, sunset and night time periods for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	106
IV-3. Relative abundance of small mammal populations in 4 habitat types in winter 1986-1987, on the Oak Ridge Reservation, east Tennessee.	111
A-1. Duration of radio-tracking, number of locations, and fate for 13 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.	157

PART I

INTRODUCTION

Habitat requirements and range of gray foxes (Urocyon cinereoargenteus), past and present, are a clue to its tremendous versatility, adaptability and success. The fossil record indicates ancestral Urocyon species may date back as far as 3.3 million years before present (Kurtén and Anderson 1980). Known fossils of U.cinereoargenteus may date as far back as the Aftonian interglacial or Kansan glacial (900,000 to 700,000 before present). Currently the gray fox ranges from extreme southern Canada through North and Central America to northern Venezuela and Columbia in South America, except for the Great Plains and parts of mountainous regions in the Northwest and Rockies in the U.S. and eastern Central America (Fritzell and Haroldson 1982; Samuel and Nelson 1982).

Fossil records indicate that Urocyon originated in Central America, a transition zone between the Nearctic and Neotropical region it now ranges (Herskovitz 1972), and has been present in North America since the Pliocene (Kurtén and Anderson 1980). U. cinereoargenteus fossils have been found dating from the Pleistocene. During the Wisconsin glaciation the gray fox reached its northern limit in Pennsylvania (Fritzell and Haroldson 1982). A range expansion northward and eastward may have occurred during the warming trend of the Hypsithermal period (5000-2000 B.C.) and contracted southward again with subsequent cooling periods. Such a pattern may have occurred more

than once (Dorf 1959; Waters 1964). The gray fox's current range appears to be restricted by cool climates and boreal forests in the north, and by cool, mountainous regions and unforested plains in the northwest and northern Great Plains (Fritzell and Haroldson 1982). Apparently, physiological constraints superimposed by temperature extremes or drought may be important factors in determining the range limits of gray foxes.

Studies indicate that gray fox habitat requirements are cosmopolitan. In general the species is closely associated with brushy, wooded areas on rocky, rough terrain (Trapp and Hallberg 1975). In the Pacific states Grinnell et al. (1937) reported that gray foxes inhabit the Upper Sonoran life zone and transition zones, including chapparal-oak covered foothills below 2288 m. This corresponds somewhat to gray fox habitat in Latin America, which includes chaparral, oak or pinyon-juniper woodlands and rock hillsides (Trapp and Hallberg 1975), and Utah as reported by Trapp (1978), which includes pinyon-juniper, black brush, and brushy and open meadows.

In the eastern United States, the gray fox is closely associated with deciduous forest (Trapp and Hallberg 1975; Follmann 1973; Yearsley and Samuel 1980). Although cultivated areas per se appear to be less optimal for gray foxes, "edge" created by the interspersation of woods and cultivated fields appears to be excellent habitat (Wood et al. 1958). This may be in part due to the high productivity of "edge" regarding rodents, rabbits, fruits and insects, all important components of the omnivorous gray fox's diet (Trapp and Hallberg 1975). The western range limit of the gray fox along the Great Plains

corresponds roughly to that of cottontails (Sylvilagus floridanus) (Hoffman and Jones 1970), a major prey item (Trapp and Hallberg 1975). Palmer (1956) suggested that the recent reappearance of gray foxes in southern Ontario and the northeast is due to the range extension and increased numbers of S. floridanus and S. transitionalis as a result of increased conversion of forest to agricultural lands.

The relationship between habitat productivity, or resource dispersion and home range size/habitat use has long been of interest. Several authors have suggested that after removing the effect of body size and metabolic needs on home range size, primary consumers require smaller home range sizes than carnivorous animals (Burt 1943; McNab 1963; Harestad and Bunnell 1979; MacDonald 1980; Gittleman and Harvey 1982). Moreover, within the order Carnivora, a significant positive relationship exists between home range size and the proportion of flesh in the diet (Gittleman and Harvey 1982). This relationship is attributed to a higher density of primary than secondary production (prey) per unit area (Harestad and Bunnell 1979). Most studies have demonstrated this relationship based on interspecific comparisons. Gray foxes in some areas provide an excellent vehicle for studying this proposed relationship within a single species. Although generally omnivorous, they may switch dietary trophic (hence density in available prey) levels across seasons, depending on available foods (e.g. the current study, part II).

Reported gray fox home range sizes vary from 0.13 km² (Richards and Hine 1953) to 10.48 km² (Wooding 1984), but patterns relating to geography/presumed habitat productivity are not readily apparent.

Differences in home range sizes relating to individual disposition, sex, age and density, as well as difficulties involved in teasing apart habitat features and seasonal utilization (e.g. denning or breeding) versus food availability further confound attempts to resolve this issue.

The influence of competition and predation on gray fox density or distribution is little understood. Grinnell et al. (1937) reported predation on adult gray foxes by golden eagles (Aquila chrysaetos), bobcats (Lynx rufus), and coyotes (Canis latrans), and mentioned that larger hawks may occasionally prey upon pups. Avoidance of coyotes by red foxes (Vulpes vulpes) has been reported (Voight and Earle 1983; Wooding 1984), although Wooding (1984) radio-tracked gray foxes and coyotes in Alabama and Mississippi with overlapping home ranges. Predation on red foxes by coyotes also has been noted, and coyotes might hold gray fox populations in check where they are sympatric (Goldman 1930; Edward Hill, pers. comm. 1986). A significant overlap in diet (Voight and Earle 1983; King 1981) might exert a further competitive influence between these canids, although differences in foraging strategies could reduce potential competition (King 1981).

Whether the presence of predators or competitors, climate and habitat, or relative occurrence of food items such as fruit and animal prey species associated with geographical range are limiting factors for gray foxes is difficult to ascertain since these factors are interrelated. Such knowledge is of value for better management of this economically valuable furbearer, as well as for improved rabies and other disease control (Samuel and Nelson 1982). Additionally, an

increased understanding of food habits, home range and habitat utilization by gray foxes in diverse geographical areas and habitats may provide insight into the interrelationships between these ecological factors, and into the tremendous versatility and success of this species.

Therefore, the objectives of this study were to obtain baseline data on gray fox ecology, including: (1) determine the seasonal food habits of gray foxes on the ORR; (2) determine the seasonal home range size of gray foxes; (3) determine the activity patterns and habitat utilization by gray foxes; and (4) attempt to discern interrelationships between seasonal food habits (trophic dietary switches) and home range size, habitat use and activity patterns.

LITERATURE CITED

- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24:346-352.
- Dorf, E. 1959. Climatic changes of the past and present. *Contrib. Mus. Paleontol. Univ. Michigan* 13:181-210.
- Follman, E.H. 1973. Comparative ecology and behavior of red and gray foxes. PhD thesis, Southern Illinois Univ., Carbondale. 152pp.
- Fritzell, E.K., and K.J. Haroldson. 1982. *Urocyon cinereoargenteus*. *Mammal. Sp. Acct.* 189:1-8.
- Gittleman, J.L., and P.H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.* 10:57-63.
- Goldman, E.A. 1930. The coyote-archpredator. *J. Mammal.* 11:325-334.
- Grinnell, J., J.S. Dixon, and J.M. Linsdale. 1937. Fur-bearing mammals of California. Vol. II. Univ. of Calif. Press, Calif. Pages 377-777.
- Hall, E.R. 1981. The mammals of North America. 2nd ed., Vol. II. John Wiley and Sons, N.Y. Pages 601-1175.
- Harestad, A.S., and F.L. Bunnell. 1979. Home range and body weight- a reevaluation. *Ecology* 60:389-402.
- Hershkovitz, P. 1972. The recent mammals of the neotropical region: a zoogeographic and ecological review. In A. Keast, F.C. Erk, and B. Glass, eds. *Evolution, mammals and southern continents*. State Univ. of N.Y. Press, N.Y.
- Hill, Edward P. 1986. Personal communication to Katie Greenberg. Department of Wildlife and Fisheries, Mississippi State University.
- Hoffman, R.S., and J.K. Jones, Jr. 1970. Influence of late-glacial and post-glacial events on the distribution of recent mammals on the Northern Great Plains. Pages 355-394 in W. Dort, Jr., and J.K. Jones, Jr., eds. *Pleistocene and recent environments of the Central Great Plains*. The Univ. Press of Kansas, Kansas.
- King, A.W. 1981. An analysis of the winter trophic niches of the wild canids of northeast Arkansas. M.S. thesis, Arkansas State Univ. 117pp.
- Kurtén, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia Univ. Press, N.Y. 432pp.

- MacDonald, D.W. 1980. Resource dispersion and the social organization of the red fox (Vulpes vulpes). Pages 918-949 in Chapman, J.A., and D. Pursley, eds. Worldwide furbearer conference proceedings, Vol. II. Frostburg, Md.
- McNab, B.K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 97:133-140.
- Palmer, R.S. 1956. Gray fox in the northeast. Maine Field Nat. 12:62-70.
- Richards, S.H., and R.L. Hine. 1953. Wisconsin fox populations. Wisc. Conserv. Dept. Tech. Wildl. Bull. 6. 78pp.
- Samuel, D.E., and B.B. Nelson. 1982. Foxes. Pages 475-490 in Wild mammals of North America. J.A. Chapman, and G.A. Feldhamer, eds. The Johns Hopkins Univ. Press, Balt.
- Trapp, G.R. 1978. Comparative behavioral ecology of the ringtail (Bassaricus astutus) and gray fox (Urocyon cinereoargenteus) in southwestern Utah. Carnivore 1:3-32.
- Trapp, G.R., and D.L. Hallberg. 1975. Ecology of the gray fox. Pages 164-178 in M.W. Fox, ed. The wild canids. Van Nostrand Reinhold Co., N.Y.
- Voight, D.R., and B.D. Earle. 1983. Avoidance of coyotes by red fox families. J. Wildl. Manage. 47:852-857.
- Waters, J.H. 1964. Red fox and gray fox from New England archeological sites. J. Mammal. 45:307-308.
- Wood, J.E., D.E. Davis, and E.V. Komareck. 1958. The distribution of fox populations in relation to vegetation in south Georgia. Ecology 39:160-162.
- Wooding, J.B. 1984. Coyote food habits and the spatial relationship of coyotes and foxes in Mississippi and Alabama. M.S. thesis, Mississippi State Univ. 43pp.
- Yearsley, E.F., and D.E. Samuel. 1980. Use of reclaimed surface mines by foxes in West Virginia. J. Wildl. Manage. 44:729-734.

PART II

GRAY FOX FOOD HABITS

ABSTRACT

Examination of 170 gray fox (Urocyon cinereoargenteus) scats collected between Sept. 1986 and Sept. 1987 on the Oak Ridge Reservation in east Tennessee revealed that plant foods were utilized most heavily, followed by invertebrate and animal prey. Proportions of the 3 categories utilized were not evenly distributed among months and were probably dictated by availability. Biological seasons were determined by detection of significant shifts in diet between the 3 food categories. Animal prey, predominantly rabbits and rodents, comprised 67.0% of winter (Jan.-April) dry weight (100% occurrence); arthropods, predominantly 17-year locusts (Magicalicada sp.), comprised 96.1% of spring (May) dry weight (275% occurrence); plant material, predominantly persimmon, cherry, blackberry and squaw-root, comprised 92.9% of summer-fall (June-Dec.) dry weight (161.6% occurrence). This study suggested that gray foxes may switch dietary trophic level depending on seasonal food availability.

INTRODUCTION

Numerous studies of gray fox (Urocyon cinereoargenteus) food habits indicate the opportunistic and omnivorous nature of these

carnivores (Hockman and Chapman 1983; Scott 1955; Nelson 1933; Errington 1935; Kozicky 1943; King 1981; Glover 1949; Wood et al. 1958; Yoho and Henry 1972; Ashby 1974; Trapp 1978). Most studies show that food availability, abundance, and season play a major role in diet composition (Trapp and Hallberg 1975). Seasonal analyses suggest dietary emphasis on mammals in the winter (King 1981; Nelson 1933; Errington 1935; Wood et al. 1958; Scott 1955; Glover 1949), while arthropods (especially orthopterans) and plant materials become important dietary components in spring, summer and autumn months (Wood et al. 1958; Kozicky 1943; Hockman and Chapman 1983; Glover 1949; Trapp 1978). Knowledge of seasonal dietary habits is important in assessing the biological needs of a species. It is also of importance in understanding habitat use, and the relationship between dietary trophic level and home range size (Gittleman and Harvey 1982) within a single species.

Although the trends observed in the above studies are almost surely correct, nonbiological determination of "season" allows for a great deal of error in interpretation of gray fox seasonal food habits, and comparison between studies. For example, Hockman and Chapman (1983) title "autumn" September-November and "winter" December-February in the Appalachian and Piedmont provinces of Maryland; Wood et al. (1958) refer to April-September as "summer" and October-March as "winter" in Georgia; Scott (1955) titles winter January-March in Iowa; Nelson (1933) titles winter December-March in Virginia; Kozicky (1943) refers to September-November as "late summer and early fall"; Ashby (1974) contrasts fall and winter combined, with spring and summer

combined. Other studies do not specify seasons except by vague reference (e.g. Glover 1949; Yoho and Henry 1972; Kozicky 1943). Determination of seasons would be more meaningful if months of similar food habit (e.g. fruit, insect or animal prey consumption) were statistically detected, and grouped into biological "seasons".

Three common methods for food habits assessment through stomach or scat analysis include frequency of occurrence, percent volume and percent weight of food items (Korschgen 1971; Lockie 1959). No method is ideal, but consistency in error is key for a satisfactory assessment of food habits (Lockie 1959). Each method may be misleading as to the the quantity of various food items consumed. Frequency of occurrence is misleading, since no distinction is made between high and low proportions of the food items consumed (Lockie 1959; Trapp 1978). The ratio of number of prey items consumed to number detected in scats often underestimates prey consumption (Lockie 1959; Murie 1946). Johnson and Hansen (1979) suggest that microscopic scat analysis may avoid this problem. Food items with high digestibility (such as a chicken, with a high flesh content) are less likely to be detected than those with low digestibility (such as a mouse, with many, small bones) (Scott 1941; Murie 1946; Weaver and Hoffman 1979). Additionally, a single food item with low digestibility may be detected in several scats, while a food item with high digestibility may be detected in only one scat (Scott 1941; Weaver and Hoffman 1979). Nonetheless, Johnson and Hansen (1979) and Scott (1941) determined frequency of occurrence to be a reliable method for food habit assessment by scat analysis.

Percent volume and percent dry weight estimates also may be misleading. It has been shown that different mammalian prey species (and sizes) may have differential dry weight digestibilities (Scott 1941; Lockie 1959; Weaver and Hoffman 1979; Murie 1946; Floyd et al. 1978). Volumetric and weight comparisons among food categories (plant, mammal, bird, reptile, and arthropod) are further complicated, since each category is proportionately differentially digested (Johnson and Hansen 1979). Johnson and Hansen (1979) estimated that dry matter digestibilities for mammals, reptiles, birds, arthropods and plant materials are about 80%, 80%, 60%, 50% and 0%, respectively in coyotes; they calculated a correction factor for estimating the original dry weight biomass of food items consumed. Lockie (1959) concluded that of frequency of occurrence, relative estimated bulk and weight of undigested matter, the latter provides the greatest consistency in error, allowing correction factors to be applied with confidence for determination of original prey weight consumed. With or without a correction factor, digestibility within a given food category is constant across seasons. Comparison among relative proportions of food categories for determining seasonal changes in food habits is valid.

Other sources of error in scat analysis include: (a) inability to detect foods lacking indigestible elements (Scott 1943) and (b) the order in which prey items are eaten may affect the estimate (Lockie 1959).

Since the objective of this study was not energetics, but simply an annual and seasonal assessment of gray fox food habits, an estimate of the relative proportion of food categories (animal, plant, and

arthropod) intake for each season was considered sufficient. As indicated from the above discussion, dry weights are not necessarily comparable between food categories. Assuming that the errors discussed above are constant for all seasons for each separate food category, comparison of the relative proportion of each independent food category among seasons should reveal major shifts in diet within a category. Overlaying the three categories might reveal dietary shifts between categories as well, despite scaling problems.

STUDY AREA

The National Environmental Research Park (NERP), Department of Energy Oak Ridge Reservation (DOE, ORR), is located approximately 28 km west of Knoxville, Tennessee, and is operated by Martin Marietta Energy Systems. The NERP comprises approximately 50 km² of the Reservation's total 144 km². The study area was located within the NERP and lies between approximately 84° 16' to 84° 21' west longitude and 35° 56' to 35° 58' north latitude.

The NERP contains a diversity of vegetation community types. These include both natural and managed yellow pine forests, eastern red cedar barrens, oak-hickory forests, bottomland hardwood forests, and old fields, as well as several developed facilities for energy research and production. The Tennessee Valley Authority's Melton Hill Reservoir and Watts Bar lake which fringe the Reservation on the west, south and east, and numerous streams and springs throughout the area provide an abundance of wetland habitat and water for a variety of wildlife

species. Several main and dirt roads dissect the Reservation, providing excellent vehicle access to most areas and tremendous advantage in gathering radio-telemetry data.

The geology of the Reservation is characteristic of the Southern Appalachian Ridge and Valley province. Parallel, southwest-northeast-oriented ridges separated by valleys (elevation ranging from 226 to 413 m above sea level) lend additional diversity to the landscape.

The DOE ORR has been protected from hunting and trapping since its purchase in 1942 until 1985, when managed hunts for white-tailed deer (Odocoileus virginianus) were permitted. This protection in combination with the diversity of habitat types creates ideal conditions for an abundance and variety of animal species.

METHODS AND MATERIALS

A total of 170 gray fox scats were collected along infrequently used roads throughout the study area in all months from September 1986 through August 1987. Sample size per month varied from 3 to 21 (mean=14.17). Scats were identified by shape, size, odor and their characteristic prominent location. To eliminate potential bias, no distinction was attempted between red and gray fox scats. The ratio of gray to red foxes on the study area was estimated by trapping to be approximately 3 to 1, so most scats were probably from gray foxes. Each scat was collected in a plastic baggie; date, location and condition of freshness were recorded.

Specimens were prepared for analysis following the methods of Scott (1941): each scat was soaked in warm water to soften, then washed through two sieves (10 and 35 meshes to the inch, respectively) over a glass beaker to catch any important material which might occasionally pass through. The remaining material (now free of much soluble matter) was air dried. All items were hand separated and analyzed with the assistance of a magnifying glass and/or binocular microscope (12-15X). Animal and plant food items were identified to the lowest taxonomic category possible. Arthropods were identified only to order. Seeds were identified according to Martin and Barkley (1961), and verified with a personal collection of known seeds or the extensive seed collection of Paul and Hazel Delcourt (Department of Botany, University of Tennessee). Bones and bone fragments were identified by zooarchaeologist Lynn Snyder (Department of Anthropology, University of Tennessee) using comparative faunal materials from the vertebrate osteological collection maintained by the Department of Anthropology, University of Tennessee, Knoxville. Additional dental formulae were taken from Hall (1981). Hairs were identified using comparative hair materials from Oak Ridge National Laboratory or personal study skins. Arthropods were identified to order using a field guide (Borror and White 1970), numerous 4-H guides, and the reference collection at the Department of Entomology and Plant Pathology, University of Tennessee. Food items not identifiable to taxa were categorized as unknown plant, invertebrate, or vertebrate.

Food types were recorded as percentage frequency of occurrence (the number of scats in which an item was found) and percentage dry

weight (the ratio between the weight of a specific food item and the total weight of all food items), calculated by methods described by Coman and Brunner (1972). Animal weight included bones, teeth and/or hair if present. Plant weight included seeds and grass. To maximize time efficiency and reduce error involved in minute weights of individual invertebrates, the weight of all invertebrates per scat was combined. Therefore, only percentage occurrence is recorded for individual invertebrate orders.

For statistical comparison, each food type was categorized as plant (including seeds and grass), invertebrate (primarily insects) or vertebrate (including mammal, bird, amphibian, fish, and reptile). The mean for each food category was plotted by month. An analysis of variance (ANOVA) (SAS Inst. Inc. 1985) was run with Tukey's studentized range test for detection of possible significant differences in dry weight between the three food categories for each month. Months which were not significantly different from one another were pooled and statistically contrasted against other months. In this manner three seasons (where either plant, animal or insect were most heavily used) were determined using fox diet itself (which almost certainly reflects food availability) as a biological indicator, rather than imposing calendar seasons on food habit analysis.

RESULTS AND DISCUSSION

A total of 52 identifiable food taxa occurred 548 times (including unidentified items) in 170 scats collected between 1 September 1986 and

31 August 1987 (Table II-1; Appendix Table A-1). Twenty-four identified plant taxa (including grass) comprised 78.6% of the total annual dry food weight, and occurred 227 times in 170 scats (133.5% frequency). Persimmon (Diospyros virginiana) (43.4% wt; 41.8% frequency), cherry (Prunus serotina) (20.2% wt; 12.9% frequency), blackberry (Rubus sp.) (4.0% wt; 10.6% frequency), and squaw-root (Conopholis americana) (6.3% wt; 4.7% frequency) were the most important fruit items, respectively, by frequency. Wild grape (Vitis sp.), mulberry (Morus sp.), acorn (Quercus sp.) and Carolina buckthorn berry (Rhamnus caroliniana) also occurred more than four times. Twelve invertebrate orders comprised 13.0% of total annual food by weight and occurred 243 times in 170 scats (142.9% frequency). Coleopterans (57.6% frequency), orthopterans (42.4% frequency), and homopterans (18.8% frequency), occurred most often (Table II-1; Appendix Table A-1).

Animal material comprised only 8.4% of the total annual dry food weight and occurred 78 times in 170 scats (45.9% frequency) (Table II-1; Appendix Table A-1). Annually, mammals (11 species) were most important, comprising 7.6% of the total annual dry food weight, and occurring 48 times (28.2% frequency). Rabbit (Sylvilagus floridanus) (4.0% wt; 7.1% frequency), white-tailed deer (1.7% wt; 4.7% frequency) (probably carrion from road kills), white footed mice (Peromyscus sp.) (0.2% wt; 3.5% frequency), and pine voles (Microtis pinetorium) (0.4% wt; 2.9% frequency) were the most frequently occurring mammalian species. Also of interest was the occurrence of two bats: Myotis sp. in February, and Lasiurus sp. in December. Bird remains occurred in 10 scats (0.4% wt; 5.9% frequency); none were identified to specific taxa.

Table II-1. Percent frequency, number, and percent dry weight of food categories and major food items, with taxa "nested" in preceding category or class, on an annual basis, found in 170 fox scats on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

Food Items	% Total Weight	Number of Times Occurring	% Frequency
ANGIOSPERMAE	78.6	227	133.5
Persimmon (Diospyros virginiana)	43.4	71	41.8
Cherry (Prunus serotina)	20.2	22	12.9
Blackberry (Rubus sp.)	4.0	18	10.6
Squaw-root (Conopholis americana)	6.3	8	4.7
Wild grape (Vitis sp.)	0.3	6	3.5
Other	4.4	102	60.0
INVERTEBRATA	13.0	243	142.9
Beetle (Coleoptera)			57.6
Grasshopper (Orthoptera)			42.4
Locust (Homoptera)			18.8
Beetle larvae (Coleopteran larvae)			7.1
Other			17.1
VERTEBRATA	8.4	78	45.9
MAMMALIA (MAMMALS)	7.6	48	28.2
Rabbit (Sylvilagus floridanus)	4.0	12	7.1
White-tailed deer (Odocoileus virginianus)	1.7	8	4.7
White-footed mouse (Peromyscus sp.)	0.2	6	3.5
Pine vole (Microtis pinetorium)	0.4	5	2.9
Other	1.3	17	10.0

Table II-1 (continued).

Food Items	% Total Weight	Number of Times Occurring	% Frequency
VERTEBRATA (continued)			
AVES	0.4	10	5.9
AMPHIBIA	0.2	3	1.8
OSTEICHTHYES	Trace	2	1.2
REPTILIA	0.1	1	0.6
UNKNOWN VERTEBRATA	0.1	14	8.2
TOTAL	100.0	548	322.3

*More detailed table in Appendix, Table A-1.

Amphibians comprised 0.2% of total vertebrate dry weight, and occurred 3 times (1.8% frequency). Amphibians included a leopard frog (Rana utricularia) and two salamanders (Plethodontidae). Fish (including Micropterus) comprised 0.01% of dry vertebrate weight, and occurred in 2 scats (1.2% frequency). Reptile (a colubrid snake) occurred in only 1 scat (0.1% wt; 0.6% frequency) (Table II-1; Appendix Table A-1).

Analysis of variance with Tukey's studentized range test revealed no significant differences between dry weights of the three food categories (plant, animal and invertebrate) in January ($n=3$; $F=0.87$; $p=0.4666$) February ($n=18$; $F=2.24$; $p=0.1165$), March ($n=13$; $F=2.77$; $p=0.0760$) and April ($n=8$; $F=1.19$; $p=0.3249$). A nonstatistical comparison of mean weights for each category for these months showed that animal dry weight was noticeably higher: January animal dry weight comprised 86.7% of mean total monthly weight; February animal dry weight comprised 69.1% of mean total monthly weight; March animal dry weight comprised 67.7% of mean total monthly weight; April animal dry weight comprised 56.0% of mean total monthly weight. Large variance in animal prey weights between scats may have obscured detection of significant differences during these months. They were grouped since they were the only 4 months where no significant differences between the 3 categories were detected. Dry animal weight for January-April was contrasted against other months; a significant difference ($F=23.37$; $p=.0001$) was detected, indicating that significantly more animal prey than plant or invertebrate material was consumed by gray foxes between January and April, 1987 than in other months (Figure II-1). Hence,

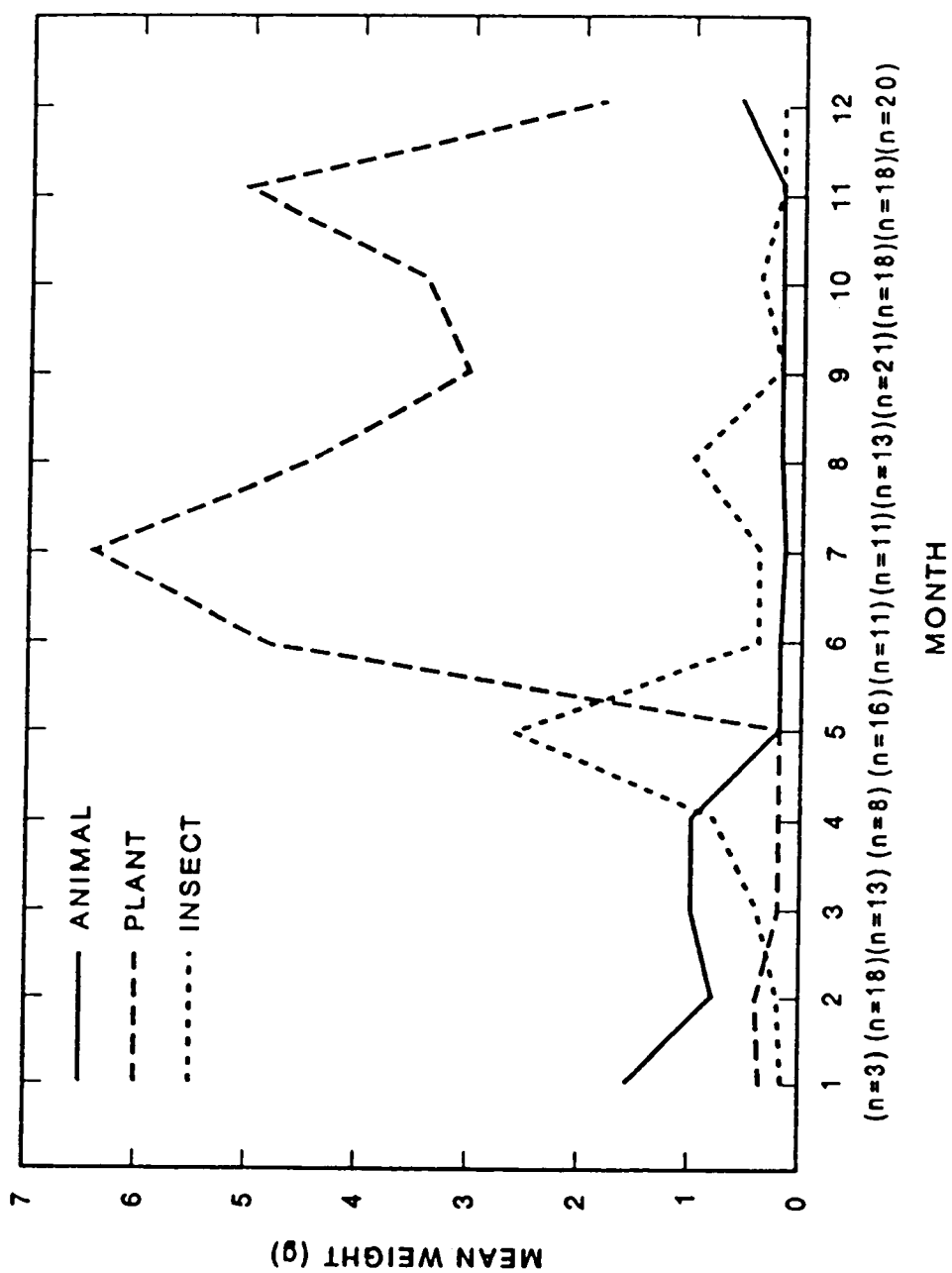


Figure II-1. Mean monthly dry weights of animal, plant, and insect material in gray fox scats, Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

January-April is referred to as winter, where animal foods were predominant in the gray fox diet.

Analysis of variance with Tukey's studentized range test determined that arthropods comprised a significantly greater ($F=33.75$; $p=0.0001$) portion of total dry weight than animal or plant material in May ($n=16$) only. A contrast between invertebrate dry weight in May versus other months revealed a highly significant difference ($F=140.15$; $p=0.0001$). Therefore, May alone is referred to as spring, where invertebrates (especially insects) were the predominant component of gray fox diet (Figure II-1).

Analysis of variance with Tukey's studentized range test revealed that plant material comprised a significantly greater portion of total dry weight than animal or invertebrate in June ($n=11$; $F=16.53$; $p=0.0001$), July ($n=11$; $F=0.67$; $p=0.001$), August ($n=13$; $F=11.68$; $p=0.0001$), September ($n=21$; $F=53.47$; $p=0.0001$), October ($n=18$; $F=26.23$; $p=0.0001$). November ($n=18$; $F=30.49$; $p=0.0001$) and December ($n=20$; $F=14.01$; $p=0.0001$). A contrast of dry plant-material weight for June-December versus other months revealed a highly significant difference ($F=72.19$; $p=0.0001$). Therefore, June-December is referred to as summer-fall, where plants were the predominant component of gray fox diet (Figure II-1).

Distribution of food categories (plant, insect and animal material) and food items within a category was not uniform among the three seasons (Appendix, Table A-2; Figure II-1; Figure II-2). Animal material comprised 67.0% of the total winter dry food weight (100.0% winter occurrence) while arthropods comprised only 18.5% (107.1%

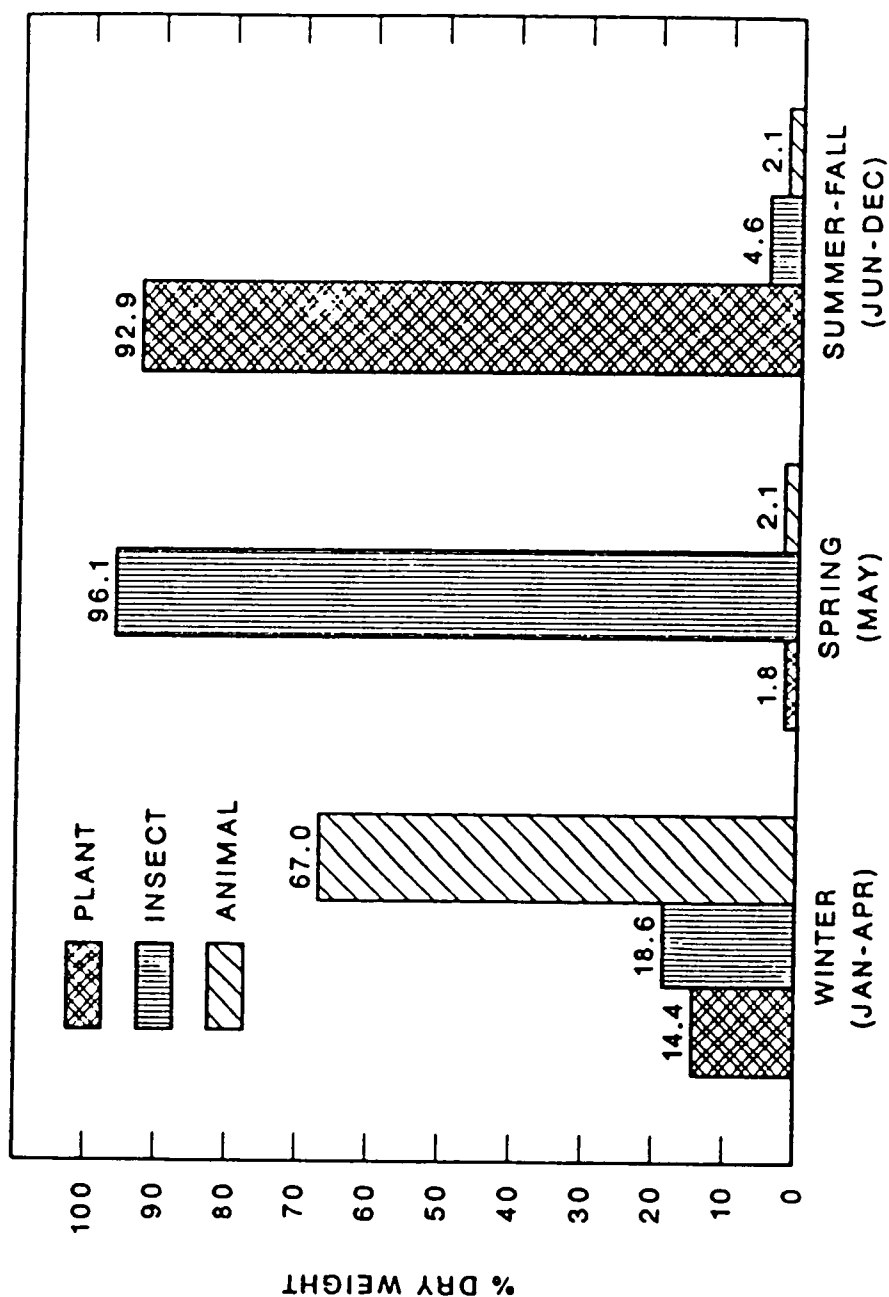


Figure II-2. Winter (n=42), spring (n=16), and summer-fall (n=112) comparison of percent dry weight of plant, insect, and animal material in gray fox scats, Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

occurrence) and plant material 14.4% (92.9% occurrence) in winter (January-April) months (n=42) (Figure II-2). Approximately 73.9% of annual total animal dry weight and 53.9% of all animal occurrences were in winter months, while only 13.2% of annual total invertebrate material (18.5% of all invertebrate occurrences) and 1.70% of annual total dry plant weight (17.2% of all plant occurrences) were in winter months. Rabbit and white-tailed deer (probably carrion) were the most frequently occurring animal food items in the winter season, followed by Peromyscus sp. and pine voles. Ashby (1974) also found these species to be the most common mammalian genera in east Tennessee gray fox diets. Coleopterans were the most frequently occurring invertebrates, while persimmon and acorn were the most frequently occurring fruit items.

Invertebrate material comprised 96.1% of the total spring dry food weight (275.0% spring occurrence) while animal material comprised only 2.06% dry weight (18.8% occurrence) and plant material 1.81% dry weight (43.8% occurrence) in spring (May) months (n=16) (Figure II-2). Of the annual total dry invertebrate weight, 57.3% occurred in the spring season (18.1% of total annual invertebrate occurrence), while only 1.89% of annual total animal dry weight (3.85% of all animal occurrences) and 0.18% of annual total plant weight (3.08% of all plant occurrences) were in spring. Homopterans were the predominant insect material occurring in May scats; this coincided with the peak emergence of the 17-year locust (Magicalicada sp.). Such an event was rare, therefore a generalization of the results of this study (spring scats as containing a predominant insect component) to other years may not be valid. Coleopterans and orthopterans also occurred frequently. Squaw-root was

the most frequently occurring spring plant food item; the only spring animal prey included one snake (Colubridae) and a chipmunk (Tamias striatus).

Plant material comprised 92.9% of the total summer-fall food weight (161.6% summer-fall occurrence), while invertebrate material comprised only 4.61% weight (137.5% occurrence) and animal material only 2.46% dry weight (29.5% occurrence) of summer-fall (June-December) months (n=112) (Figure II-2). Of annual total dry plant weight, 98.1% occurred in the summer-fall season (79.7% of annual total plant occurrence) while only 29.5% of annual total invertebrate dry weight (63.4% of total annual invertebrate occurrences) and 24.2% of annual total animal dry weight (42.3% of all animal occurrences) was in the summer-fall season (Figure II-2). The relative utilization of fruit species shifted over the 6 summer-fall season months. Squaw-root comprised the bulk of June plant weight and percent frequency of occurrence, but was present only in small quantities in all remaining summer-fall months. Blackberry was important from June through August, cherry in July and August, and persimmon became the predominant fruit item beginning in September through December. Coleopterans, orthopterans, and homopterans were most frequently occurring invertebrate food items; rabbit and bird were the most heavily utilized animal prey items in the summer-fall season (Appendix, Table A-2).

Although not quantified, the occurrence of the several fruit species in gray fox scats temporally corresponded with their ripening and availability in east Tennessee. It cannot be assumed however, that animal prey availability on the study site fluctuated significantly

between seasons (part IV). Therefore, this study suggested that foxes were taking animal prey only as a "second choice", when fruit, a more easily acquired food source, was not readily available. The spring, 1987 emergence of the 17-year locusts undoubtedly presented a unique case, perhaps artificially emphasizing categorical "jumps" in gray fox food habits among seasons in the current study.

The opportunistic use of seasonally available foods by gray foxes (as for many other canids) is often noted. The non-biological separation of seasons, and reporting methods such as frequency of occurrence, however, could obscure dramatic shifts in dietary trophic level which might occur. Trapp (1978) reported a predominance of fruit in the gray fox autumn diet in Utah, but the proportion of mammal and/or arthropod was also of some importance; similarly, arthropods were prevalent in the spring and summer diet, but not to the virtual exclusion of plant or animal food categories. While mammals comprised a large proportion of winter gray fox diet, so did fruit (Trapp 1978). Yearsley and Samuel (1980) noted that gray fox scats in October were composed almost entirely of autumn olive (Eleagnus sp.) in West Virginia. Hamilton et al. (1937) reported that some red fox scats were comprised of almost 100% fruits and berries in late summer and early fall in Massachusetts. In contrast, Wood et al. (1958) noted that rabbits, rodents and birds comprised 44% by volume of the summer (April-September) diet and 71% of the winter (October-March) diet, in north Florida, south Georgia and South Carolina. Insects accounted for 41% of summer, and 8% of winter volume. Yoho and Henry (1972), in the Appalachian mountains of east Tennessee, reported the reverse trend

from that observed in the current study. In their study, cottontails were represented more frequently in stomachs collected in summer ($n=17$) than winter ($n=7$); they suggested that peak production of young cottontails in summer might account for their increased occurrence in gray fox diet. Predation on small mammals was similar in both seasons, but predation on birds decreased in summer. Yoho and Henry (1972) also reported that less vegetative matter was consumed in summer than winter, although large quantities of debris eaten by trapped animals precluded analysis of plant foods; this may also have precluded an objective analysis of fox stomach contents. Higher elevation and less habitat diversity (hence food availability) within their study area, as well as small sample size, might also account for some of the contrast in findings with the current study. Ashby (1974) reported that mammals occurred in 74.7% of fall-winter diet and 86.3% of spring-summer gray fox diet in east Tennessee, although the occurrence of insects and vegetative matter increased in spring-summer by 27.7% and 33.9%, respectively. Nelson (1933) and Errington (1935) reported a high incidence of animal material in winter gray fox stomachs in Virginia and the mid-west, respectively.

Errington (1935) suggested that fox food habits seem to be heavily dependent on prey availability, but noted that small mammals appeared to be a year-round food staple, with other kinds of prey fluctuating according to seasonal availability, weather, prey vulnerability, abundance and experience of individual foxes. The current study confirmed the opportunistic feeding habits of gray foxes, but suggested

that animal prey was exploited only in absence of other more easily acquired food sources.

SUMMARY AND CONCLUSIONS

Gray fox scats collected in East Tennessee, 1986-1987, consisted most heavily of plant material, followed by invertebrate (especially insect) and animal prey. Relative proportions of each category were not constant between months, signifying the importance of describing seasons in a functional sense rather than by arbitrary, categorical delineation. Animal prey comprised 67.0% of total winter (January-April) dry food weight and occurred with 100.0% frequency; insect material comprised 96.1% of spring (May) dry weight and occurred with 275.0% frequency; plant material comprised 92.9% of summer-fall (June-December) dry weight and occurred with 161.6% frequency.

Although generally omnivorous, this term used in the conventional sense, to describe gray fox food habits within a season or at a given time interval, is misleading. Given extreme and distinct differences in the relative proportion of each food category among biologically determined seasons, gray fox food habits may be more aptly described as shifting dietary trophic levels from carnivore (winter) to insectivore (spring) to frugivore (summer-fall). Since such dramatic dietary shifts were almost certainly a response to the seasonally shifting availability of fruits and invertebrates, heavy winter exploitation of animal prey relative to spring and summer-fall indicated that this prey source may

be a "last resort". Seasonal exploitation of the most abundant and easily acquired food sources indicates that the gray fox may indeed be the hallmark of opportunism.

LITERATURE CITED

- Ashby, J.R. 1974. Food habits and distribution of the red fox (Vulpes fulva, Desmarest) and gray fox (Urocyon cinereoargenteus, Schreber) on the Catoosa WMA, Tennessee. M.S. thesis, Tennessee Tech. Univ. 84pp.
- Borrer, D.J., and R.E. White. 1970. Insects of America north of Mexico. Houghton Mifflin Co., Boston, Massachusetts. 404pp.
- Coman, B.J., and H. Brunner. 1972. Food habits of the feral house cat in Victoria. J. Wildl. Manage. 30:848-853.
- Errington, P.L. 1935. Food habits of mid-west foxes. J. Mammal. 16:192-200.
- Floyd, T.J., L.D. Mech, and P.A. Jordan. 1978. Relating wolf scat content to prey consumed. J. Wildl. Manage. 42:528-532.
- Gittleman, J.L., and P.H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. Behav. Ecol. Sociobiol. 10:57-63.
- Glover, F.A. 1949. Fox foods on West Virginia wild turkey range. J. Mammal. 30:78-79.
- Hall, E.R. 1981. The mammals of North America. Vol. II, 2nd ed. John Wiley and Sons, N.Y. Pages 601-1175.
- Hamilton, W.J. Jr., N.W. Hosley, and A.E. MacGregor. 1937. Late summer and early fall foods of the red fox in central Massachusetts. J. Mammal. 18:366-367.
- Hockman, J.G., and J.A. Chapman. 1983. Comparative feeding habits of red foxes (Vulpes vulpes) and gray foxes (Urocyon cinereoargenteus) in Maryland. Am. Midl. Nat. 110:276-285.
- Johnson, M.K., and R.M. Hansen. 1979. Estimating coyote food intake from undigested residues in scats. Am. Midl. Nat. 102:363-367.
- King, A.W. 1981. An analysis of the winter trophic niches of the wild canids of northeast Arkansas. M.S. thesis, Arkansas State Univ. 117pp.
- Korschgen, L.J. 1971. Procedures for food-habits analyses. Pages 233-250 in Giles, R.H., ed. Wildlife management techniques. 3rd ed. The Wildlife Society, Washington D.C.
- Kozicky, E.L. 1943. Food habits of foxes in wild turkey territory. Pennsylvania game news. 14:8-9, 28.
- Lockie, J.D. 1959. The estimation of the food of foxes. J. Wildl. Manage. 23:224-227.

Martin, A.C., and W.D. Barkley. 1961. Seed identification manual. University of Calif. Press, Berkeley. 221pp.

Murie, O.J. 1946. Evaluating duplications in coyote scats. J. Wildl. Manage. 10:275-276.

Nelson, A.L. 1933. A preliminary report on the winter food of Virginia foxes. J. Mammal. 14:40-43.

SAS Institute Inc. 1985. SAS user's guide: statistics. Version 5 edition. Cary, N.C: SAS Institute Inc. 956pp.

Scott, T.G. 1941. Methods and computations in fecal analysis with reference to the red fox. Iowa State Coll. J. Sci. 15:279-285.

-----, 1943. Some food coactions of the northern plains red fox. Ecol. Monog. 13:427-479.

-----, 1955. Dietary patterns of red and gray foxes. Ecology 36:366-367.

Trapp, G.R. 1978. Comparative behavioral ecology of the ringtail and gray fox in southwestern Utah. Carvivore 1:3-32.

-----, and D.L. Hallberg. 1975. Ecology of the gray fox. Pages 164-178 in M.W. Fox, ed. The wild canids. Van Nostrand Reinhold Co., N.Y.

Weaver, J.L., and S.W. Hoffman. 1979. Differential detectability of rodents in coyote scats. J. Wildl. Manage. 43:783-786.

Wood, J.E., D.E. Davis, and E.V. Komarek. 1958. The distribution of fox populations in relation to vegetation in southern Georgia. Ecology 39:160-162.

Yearsley, E.F., and D.E. Samuel. 1980. Use of reclaimed surface mines by foxes in West Virginia. J. Wildl. Manage. 44:729-734.

Yoho, N.S., and V.G. Henry. 1972. Foods of the gray fox (Urocyon cinereoargenteus) on European wild hog (Sus scrofa) range in east Tennessee. J. Tenn. Acad. Sci. 47:77-79.

PART III

GRAY FOX HOME RANGE, DENSITY, AND TERRITORIALITY

ABSTRACT

Gray fox (Urocyon cinereoargenteus) home range sizes were determined from radio-telemetry data (Sept. 1986-Aug. 1987) on the Oak Ridge Reservation, east Tennessee. Minimum density was estimated at 0.45 adult foxes per km². Average composite home range size was 3.97 km² for 10 foxes (4.41 km² for 6 adults and 3.32 km² for 4 subadults). No significant differences were detected between composite home range sizes for males and females or between adult and subadult foxes. Seasonal home range sizes were tested for differences based on seasons of high (spring-fall: insect and fruit prey) and low (winter: animal prey) food availability, and breeding-cycle (breeding, pup-rearing and prebreeding). Statistical analysis detected no significant differences among seasons, probably due to high variability between individual foxes. Changes in home range size among seasons for individual foxes did not correspond to any obvious pattern or environmental influence. Territoriality and monogamy were suggested by closely coinciding home ranges of adult male and female pairs, with little overlap between adult males or adult females. Extensive overlap of home ranges by subadult foxes (female, in this case) with one adult male fox indicated that family aggregations may occupy the same home range. Despite seasonally differential area-utilization, boundaries for composite home

ranges seemed to be recognized by neighboring foxes year-round; "core areas" within home ranges remained relatively constant. It is suggested that maintaining territories containing sufficient year-round resources is advantageous in areas of periodic food scarcity (winter, in this case). It is hypothesized that territory sizes may be adjusted to contain a year-round food supply.

INTRODUCTION

Previous studies have revealed widely variable home range sizes for gray foxes (*Urocyon cinereoargenteus*) both within and between populations. Few patterns in home range size seem to emerge in relation to geographic location or presumed habitat productivity. Yearsley and Samuel (1980) estimated home ranges for 3 male gray foxes averaging 0.97 km^2 and 0.75 km^2 for one female gray fox in rolling farmland and wooded, mountainous terrain in West Virginia. In an area of mixed habitat types with gentle to steep topography in east central Alabama, home ranges for male gray foxes averaged 6.53 km^2 and 6.26 km^2 for females (Nicholson 1982). In the Zion National Park, southwest Utah, home range size averaged only 1.02 km^2 for 4 males and 1.13 km^2 for 4 females (Trapp 1978). Fuller (1978) estimated an average of 1.22 km^2 for female gray foxes in California. Hallberg and Trapp (1984), working in less diverse habitat near Fuller's study site estimated a mean home range of 1.29 km^2 (range $1.06\text{-}1.72 \text{ km}^2$) for 2 male and 2 female gray foxes. Haroldson and Fritzell (1984) estimated monthly home ranges of $2.99 \pm 1.55 \text{ (SD) km}^2$ and composite home ranges of $6.76 \pm$

3.57 km² in mixed habitat in the Missouri Ozarks. Richards and Hine (1953) estimated home ranges of 0.13-3.10 km² in a mixed woodland and agricultural area in rolling topography in southwestern Wisconsin. Wooding (1984) estimated home range sizes ranging from 1.15-7.22 km² for 8 gray foxes in an area of 70% agriculture and 30% mixed wooded area and some commercial pine plantations in Alabama, and 2.29-10.48 km² for 3 gray foxes in a predominantly wooded area in Mississippi (mean for pooled study site estimates was 4.93 km²).

Numerous inconsistencies among home range studies make comparisons difficult, and patterns difficult to discern. Differences in animal sample size, number and sampling regime of radio-telemetry locations, methods for calculating home range (Dunn 1977; MacDonald et al. 1979; Smith et al. 1981; Laundré and Keller 1984; Bekoff and Mech 1984; Boyle 1986) and subjective exclusion of locations (Ables 1968; Andelt and Gipson 1979) may affect results. In addition, seasonal changes in home range size within an individual or population frequently go undetected, since animals are monitored over different months and for varying lengths of time.

The distinction between "territory" and "home range" is often an additional source of confusion in comparing studies, since the terms are often used interchangeably. A territory is defined as a fixed and exclusive area and/or resource, defended by an individual or group from intruders, whether by aggression or advertisement such as scent marking or vocalizations (Kaufmann 1983; Brown and Orians 1970). A home range is simply the area in which an individual normally lives, (Brown and Orians 1970; Burt 1943), and is not defined on the basis of specific

behaviors, nor exclusion of other individuals (Brown and Orians 1970).

Since the definition of territoriality includes resource defense, a prerequisite then, is the defensibility (distribution) of resources (Brown 1975; MacDonald 1983). Since time and energy costs of territorial defense may be high (Kaufmann 1983; Mace et al. 1983), advantages conferred must be great. Overlapping territories (and home ranges) may be more common then, where resources are abundant (Jonkel and Cowan 1971; MacDonald 1980, 1983), and could explain some intra-species differences in space-utilization between studies.

Advantages of territoriality may include exclusive access to food resources and the "certainty" conferred in familiarity with location and quantity of those resources (Mace et al. 1983). This, in turn may improve chances for survival and reproductive success, or "fitness" (e.g. Lack 1966; Brown and Orians 1970; Brown 1975; Messier and Barrette 1981; von Schantz 1981, 1984a; Kaufmann 1982). Other advantages may include access to mates, shelter, distance from intraspecies-communicated disease and parasites, or other factors (Brown and Orians 1970).

Evidence for territoriality in gray foxes has been noted in several studies. Lord (1961) reported that gray fox "family aggregations" appeared to be spatially segregated from other family units in north Florida. Trapp (1978) described non-overlapping, adjacent home ranges for 4 male gray foxes in Zion National Park, Utah. Follmann's (1973) research also indicated that gray foxes are territorial, as did the present study (to be discussed). Hallberg and Trapp (1984), however, described nearly coinciding home ranges and

activity centers for 2 male and 2 female (ages unspecified) gray foxes, suggesting that territoriality was not occurring.

Behavioral evidence of territoriality in gray foxes is scanty. Trapp (1978) observed 2 apparent agonistic encounters between gray foxes. Use of urine and scats may be important in marking territories. Scats are commonly left in prominent locations along roads and trails, often in small concentrations (Grinnell et al. 1937; Wood et al. 1958; Richards and Hine 1953; Trapp 1978; observations in the present study). Most studies on gray foxes refer to any regular space-utilization as "home range". Since no definitive evidence for territoriality in gray foxes exists, the term "home range" will be used in the following discussion unless the implications of territoriality are specifically intended.

Several factors influencing home range size have been suggested. Sex, age and season are thought to play role (Burt 1943; Harestad and Bunnell 1979), as might interspecific and/or intraspecific competition (Samuel and Nelson 1982). Natural features of the landscape, such as rivers or lakes, also might influence home range size and shape (Samuel and Nelson 1982).

Home range sizes of female foxes may vary with breeding (increase), whelping (decrease), and prebreeding (increase to an intermediate level) seasons (Follmann 1973). Young (dispersing) and adult males also may travel widely in the fall and winter, probably in relation to breeding (Sheldon 1950; MacDonald 1980). From a descriptive, qualitative comparison, differences in home range size between sexes have been related to sexual-social systems in carnivores.

While both sexes in monogamous species (e.g. canids) tend to have similar-sized home ranges, males of promiscuous species (e.g. felids) have much larger home ranges, presumably overlapping with several potentially receptive females (Kleiman and Eisenberg 1973).

Other authors (Lockie 1966; Trapp and Hallberg 1975; Clutton-Brock and Harvey 1979; Springer 1982; Burt 1943) have suggested that population density might be negatively correlated with home range size. Unfortunately, too few studies report gray fox densities along with home range estimates. In addition, most studies report densities on areas that are annually trapped. Densities reported for gray foxes range from 0.38 per km² on California chaparral land prior to trapping season (Grinnell et al. 1937), 1.35 per km² in northern Florida (Lord 1961), 1.92-4.62 per km² in Ohio (Gier 1948), to 10.38 per km² in southern Wisconsin in December, 1932 (Errington 1933). The present study provided the opportunity to estimate population densities in relation to home range movements in an area relatively unaltered by human impact.

While home range sizes may vary with population density then, population density may in turn vary according to habitat productivity and resource dispersion (Clutton-Brock and Harvey 1979; MacDonald 1980, 1983). This is partly due to a lower carrying capacity in less productive habitats. In addition, animals may require larger home ranges (or territories) where resources are widely dispersed or scarce. This may result in some "homeless" individuals, or individuals forced to live within territories belonging to others, or in marginal areas at the sacrifice of their own reproductive success (Brown and Orians 1970;

Kaufmann 1983; von Schantz 1981, 1984a). Hence habitat productivity and resource dispersion may ultimately influence both population density and home range (or territory) size.

The influence of food availability (Springer 1982; Trapp and Hallberg 1975) and dispersion (MacDonald 1980, 1983) on home range size in foxes has been suggested. Fuller (1978) thought that gray fox home range size was more closely related to the quality and distribution of habitat types than other factors. Seasonal changes in gray fox home range size frequently have been noted (Nicholson 1982; Richards and Hine 1953), with a size increase in late fall and winter often attributed to decreasing food availability. An inverse relationship between prey density and home range size was reported for lynx (Lynx canadensis) in the southwestern Yukon (Ward and Krebs 1985), bobcats (Felis rufus) (Litvaitis et al. 1986), tigers (Panthera tigris) (Sunquist 1981), and lions (Panthera leo) (van Orsdol et al. 1985). Flexibility in area size utilized over time suggests "home range" rather than fixed, defended territories, although smaller territories unrelated to food resources might be contained within home ranges (Brown and Orians 1970).

While changes in home range size may be one response to fluctuations in food availability, other researchers have reported no such relationship (Kaufmann 1983; Mace et al. 1983). Lynx in Rochester, Alberta, for example, were observed to switch to an alternate food source (especially carrion) rather than expand their territories in response to a fall in prey population levels (Brand et al. 1976). Similarly, Messier and Barrette (1981) observed no changes in coyote (Canis latrans) territory sizes despite dramatic changes in

prey availability. Lockie (1966) reported no adjustment of weasel (Mustela nivalis) territory sizes to fluctuations in prey numbers. Kruuk and Parish (1982) found that the size of Eurasian badger (Meles meles) territories was correlated with the distance between feeding patches. MacDonald (1980, 1983) observed a similar phenomenon in red foxes (Vulpes vulpes), and arctic foxes (Alopex lagopus) (Hersteinsson and MacDonald 1982). These authors reported that while fox home range sizes remained constant, each was adjusted to include a similar area of productive habitat (residential area for red foxes; coastline for arctic foxes), suggesting the importance of resource dispersion in influencing territory (or home range size). MacDonald (1980, 1983) suggested that territory size is positively related to resource dispersion, and is adjusted to contain a sufficient food supply during periods of scarcity. Such a strategy provides some insurance of survival in "worst-case scenarios", and eliminates any need to alternate the size of any given territory in response to changes in food availability.

On an interspecific basis, the relationship of body size, metabolic needs and dietary trophic level to home range size has long been noticed. Seton (1909 in Burt 1943) commented that "the size of this home region corresponds somewhat with the size of the animal. Flesh-eaters as a class have a larger home region than herb-eaters". As in the above studies which address home range size in relation to intra-trophic level variation in prey density, this relationship is attributed to the diminishing density of food resources with ascending trophic levels.

McNab (1963) demonstrated a relationship between body weight, diet, and home range size in small mammals; he determined that "hunters" (seed, fruit, and nut eaters) who must search over distances for their food have larger home ranges than "croppers" who eat vegetation within a smaller area. Mace et al. (1983) demonstrated this relationship for several species of vertebrates. Schoener (1968) found that territory size for a given body weight was highest for carnivorous bird species (who feed higher on the food pyramid, therefore on a less abundant food source) and lowest for those species feeding on a relatively abundant resource (herbivores). A higher energy expenditure involved in predation relative to "cropping" also might contribute to the need for larger home range sizes in carnivorous animals (Harestad and Bunnell 1979).

Harestad and Bunnell (1979) statistically demonstrated a relationship between body weight and home range size in mammals. They found that this relationship was best described when trophic groups were treated independently, with carnivores having larger home range than omnivores or herbivores, respectively (although Harvey and Mace (1982) criticized their herbivore sample as biased, since the 4 largest species were all from the genus Odocoileus and had similar body and home range sizes). Gittleman and Harvey (1982) found that after removing the effects of metabolic needs, diet showed a significant influence on home range size in carnivores. Carnivores with a large proportion of flesh in their diets have relatively larger home ranges than predominantly fruit or insect-eating carnivores, respectively. These differences were attributed to disparities in relative density,

production and dispersion between primary and secondary trophic level food sources across the landscape (Gittleman and Harvey 1982; Harestad and Bunnell 1979).

The gray fox in east Tennessee provides a unique opportunity to study the relationship between dietary trophic level (prey density) and home range size on an intraspecific basis. An omnivore in a general sense of the word, this species may exhibit significant seasonal dietary shifts between trophic levels, with either animal prey (winter), insects (spring) or fruit (summer-fall) composing the significant majority of the diet, depending on seasonal food availability (part II). In this study, scats for food habit analysis (part II) were collected simultaneously with home range data on gray foxes, September 1986-August 1987. Therefore, the null hypothesis that seasonally differential resource dispersion, or seasons of overall resource "abundance" (primarily insect and fruit diet) and "scarcity" (primarily animal diet) did not influence home range size in gray foxes, was tested based on known shifts in dietary trophic level. The following null hypotheses were also tested: (1) home range size was not influenced by reproductive "seasons" including breeding, whelping/pup-rearing, and prebreeding; (2) home range size was not influenced by sex; and (3) home range size was not influenced by age in gray foxes. Finally, the spatial distribution of foxes in relation to reproductive units and territoriality, along with population density estimates will be discussed.

STUDY AREA

The National Environmental Research Park (NERP), Department of Energy Oak Ridge Reservation (DOE, ORR), is located approximately 28 km west of Knoxville, Tennessee, and is operated by Martin Marietta Energy Systems. The NERP comprises approximately 50 km² of the Reservation's total 144 km². The study area was located within the NERP and lies between approximately 84° 16' to 84° 21' west longitude and 35° 56' to 35° 58' north latitude.

The NERP contains a diversity of vegetation community types. These include both natural and managed yellow pine forests, eastern red cedar barrens, oak-hickory forests, bottomland hardwood forests, and old fields, as well as several developed facilities for energy research and production. The Tennessee Valley Authority's Melton Hill Reservoir and Watts Bar lake which fringe the Reservation on the west, south and east, and numerous streams and springs throughout the area provide an abundance of wetland habitat and water for a variety of wildlife species. Several main and dirt roads dissect the Reservation, providing excellent vehicle access to most areas and tremendous advantage in gathering radio-telemetry data.

The geology of the Reservation is characteristic of the Southern Appalachian Ridge and Valley province. Parallel, southwest-northeast-oriented ridges separated by valleys (elevation ranging from 226 to 413 m above sea level) lend additional diversity to the landscape.

The DOE ORR has been protected from hunting and trapping since its purchase in 1942 until 1985, when managed hunts for white-tailed deer

(Odocoileous virginianus) were permitted. This protection in combination with the diversity of habitat types creates ideal conditions for an abundance and variety of animal species.

METHODS AND MATERIALS

Trapping

Foxes were captured in No. 1.5 Victor soft-catch leg-hold traps using dirt-hole sets and drags. Attractants included fox urine, fox gland lures, pork cracklings, fish oil, and muskrat oil. Traps were concentrated on the ORR NERP along dirt roads and powerlines. The first several foxes trapped were anesthetized with 5-10 mg/kg ketamine hydrochloride (Ketaset). After it became apparent that gray foxes become submissive when grasped by the back of the neck, foxes were handled without drugs using methods adapted from Nicholson (1982). Each animal was fitted with a radio-collar equipped with a mercury tip-switch activity sensor (Telonics) in the 150.3-151.84 MHz band. Ear tags also were attached for on-sight identification.

Sex, age (juvenile or adult), and overall physical condition were noted. Body measurements taken included weight, front and hind pad length, pes, tail length, total length, girth, neck circumference and ear length. Animals were released at the trap site.

Radio Telemetry

Receiving stations (n=138) were established on the NERP based on proximity to radio-collared gray foxes, angle between stations, topography, ease of location on study-area maps, and distance from electromagnetic interference (except where unavoidable for obtaining adequate angles). Animals were located with a 4-element hand-held Yagi antenna and a Telonics portable receiver by triangulation using the "loudest signal method" (Springer 1979). An azimuth was obtained on one or more foxes from a station using a Suunto KB-14 hand-bearing magnetic compass, the vehicle quickly driven to a second station and another azimuth taken. Often 3 or more azimuths were obtained to achieve an angle as close to the 90° optimum (Heezen and Tester 1967) as possible, hence increase accuracy. Angles less than 45° and greater than 135° were discarded. Locations where poor signals, signal bounce, or too great a time lapse between bearings (> 5 minutes, or less if the animal seemed to be moving rapidly) interfered were discarded. Fox identification number, date, time, compass bearings, stations, quality of signal (if accuracy was in doubt), and activity were recorded. Initially (September-November 1986), each animal was located at 1-hour intervals one night each week between 1600-0800 hrs. When it was realized that all radio-collared foxes could be monitored on the same night with little sacrifice of information gathered (Smith et al. 1981; Dunn 1977), and with greater independence of locations (Dunn 1977) if locations were taken every 2 hours instead, this sampling regime was adopted (December 1986-August 1987). All field azimuths were converted

into X,Y coordinates by computer program "Convxpoly" (Boyle 1986) and hand plotted.

Data Analysis

Peripheral plotted fixes were outlined using the minimum convex polygon method (Mohr 1947). This is the most common method used to delineate home range boundaries (Laundré and Keller 1984), and was chosen in part to facilitate comparability between studies. The minimum convex polygon method provides stabilized area estimates for input data sets and high correlation with confidence ellipse home range area estimates. This method also has a better ability to represent irregularities in home range boundary (Boyle 1986), although accuracy of home range shape may be restricted by its strictly concave periphery (Garshelis 1983). This restriction may also artificially inflate home range size estimates, since involutions in the actual shape are ignored. In addition, this method may yield misleading results, since it rests on the assumption that the animal used all points within the home range equally (Bowen 1982).

Several researchers (e.g. Bekoff and Mech 1984; Bowen 1982; Dunn 1977; Boyle 1986) have emphasized the importance of obtaining an adequate observation sample size, since area estimates may increase asymptotically with increasing locations. Bekoff and Mech (1984) suggested that between 100-200 locations provided reliable home range area estimates for coyotes, but noted that fewer locations were often sufficient for smaller-sized species, since smaller body size often

corresponds to smaller, more easily estimated home range areas (Gittleman and Harvey 1982; Harestad and Bunnell 1979; McNab 1963; Harvey and Clutton-Brock 1981). Bowen (1982) reported that an average of 42 locations was necessary to define the size of resident coyote home range areas. Boyle (1986), using bobcat data, found that an average of 88 locations (range 51-147) was sufficient using the minimum convex polygon method for home range area estimates. Since both coyote and bobcat home ranges (and body size) are generally larger than gray foxes, even fewer observations might be sufficient for the purposes of this study.

Independence of observations is also important in order to maximize the information gained per observation (Dunn 1977). While locations taken at 2-hour intervals were considered independent, observations taken over several days per season probably insures independence. Boyle (1986) found that 4-10 days of bobcat radio-telemetry data were sufficient to attain stabilized home-range estimates. Ables (1968) found that the number of days required to adequately measure the home range sizes of red foxes varied from 5-16. By these criteria (number of locations and number of days monitored) a sufficient sample size was used for most fox-seasons in the present study (Appendix, Tables A-4 to A-6; Figure A-1).

Peripheral fixes which were subjectively determined to be outside of "that area traversed by an animal in its normal activities..." (Burt 1943) were excluded with the "atypical habitat elimination method" (Ables 1968). This method relies on "knowledge of an animal's daily travel routes and habits... to determine what (is) typical and what

(is) atypical" (Ables 1968). Springer (1982) disagrees with the exclusion of any locations, since the home ranges of coyotes radio-tracked in his study "may have been little else than core areas strung together by 'occasional sallies'". Andelt and Gipson (1979) calculated coyote home range sizes of 103% larger when all locations were included than when those deemed "exploratory movements" were omitted.

A potential for bias in calculation of home range sizes exists for either inclusion of all locations, or subjective exclusion of some locations. A knowledge of the species in question, and familiarity with the study animals is necessary to make the most valid choice in methodology. Since intense sampling enabled the observer to become familiar with the movement habits of each gray fox, and since "occasional sallies" were considered highly unusual, a subjective exclusion of some locations was considered valid in this study. All locations excluded fit the following criteria: (1) all were considered atypical (a subjective judgement based on familiarity with animal movements) of the animal in question and (2) occurred (in any one general direction) within a one week period, or perhaps one additional time. Exclusion of any locations was considered necessary only for male foxes 69 and 76, and female fox 78; trial statistics run including all locations did not change any conclusions discussed below. Home range areas were estimated using a dot grid acetate overlay, and counting acreage (Mosby 1971); all areas were converted to km^2 .

Composite home range sizes were calculated for each fox. Home range sizes also were calculated based on somewhat arbitrary breeding cycle dates (January-March for breeding; April-June for whelping/pups;

July-December for prebreeding) as reported for foxes in the southeast (Wood 1958; Sullivan 1956; Layne 1958; Nowak and Paradiso 1983).

Sample size for locations collected in May alone (range = 0-23 for each animal) was considered insufficient to yield valid home range sizes; this precluded statistical testing of the null hypothesis that there were no differences in home range size between the three dietary seasons (animal prey, fruit, and insect) (see part II) for gray foxes. Home range sizes were calculated, however, based upon seasons of food abundance (including May: predominantly insect diet, and June-December: predominantly fruit diet), and food scarcity (including January-April: predominantly animal prey) (see part II).

T-tests were run using SAS (SAS Inst. Inc. 1985) to test the following null hypotheses: (1) there was no difference between composite home range sizes for male and female gray foxes (2) there was no difference between composite home range size for adult and subadult foxes. Analysis of variance (ANOVA) (SAS Inst. Inc. 1985) was conducted to test the null hypotheses that (3) there was no difference in home range size between "scarce" and "abundant" food seasons (within and between sex) (4) there was no difference in home range size among breeding season (January-March), whelping/pup-raising season, (April-June), and prebreeding season (July-December), both within and between sexes. Where no home range estimate was available for a fox in a specific season (due to radio-transmitter failure or mortality), the mean home range for all study animals within that season was artificially inserted for computer entry to prevent the omission of the

entire data set for that fox. Hence the maximum possible sample size was maintained for each data set.

RESULTS AND DISCUSSION

Trapping

A total of 937 trapnights yielded 17 captures of 16 gray foxes. Of these, one escaped upon approach, and 2 were not collared due to trap-related injuries. Radio-collared foxes included 6 males and 7 females. Physical data on captured animals are summarized in the Appendix, Table A-3.

Home Range and Territoriality

A total of 2247 radio locations were obtained between September, 1986 and August, 1987 to estimate the home ranges of 12 gray foxes. Of the total sample, 1577 radio locations were recorded between sunset and sunrise and 670 were recorded between sunrise and sunset. Most locations were obtained nocturnally and crepuscularly, since most gray fox activity occurs during these hours (Trapp 1978; Trapp and Hallberg 1975; Yearsley and Samuel 1980; Fritzell and Haroldson 1982); for this reason, radio locations taken during full-night periods produce more realistic (often larger) home range estimates than locations taken during daylight hours alone (Smith et al. 1981). Duration of radio-

tracking, monthly number of radio locations, and the eventual fates of the 13 collared foxes are described in Appendix, Figure A-1.

For all statistical calculations, male 65 and female 80 were excluded from computations, since insufficient sample sizes were obtained for valid home range estimates. Female 63 also was excluded because her "home range" was aberrantly large (17.94 km^2 ; > 2.5 times larger than any other fox), and may not have been a "home" range at all, but instead the explorations of a young, dispersing fox. Nonetheless, such a large area estimate would have skewed the statistics so as to give misleading results.

Composite home range sizes for 12 gray foxes are summarized in Appendix, Table A-4 (illustrated in Figure III-1). Mean composite home range size for 10 gray foxes was 3.97 km^2 (range 2.09-6.91); for 5 females 3.67 km^2 (range=2.09-5.54) (Figure III-2), and 4.27 km^2 (range 2.83-6.91 km^2) for 5 males (Figure III-3). A t-test revealed no significant differences between male and female composite home range sizes ($p=0.5625$). The trend for slightly larger home range size in males was apparent, but variance among individual gray fox home range size was high.

Mean composite home range size for 6 adult gray foxes was 4.41 km^2 (range 2.83-6.91), and 3.32 km^2 (range 2.09-5.54) for 4 subadults. No significant differences were detected in home range size between adult and subadult gray foxes ($p=0.2909$).

ANOVA revealed no significant differences ($p=0.3350$) in home range size among breeding season (January-March), whelping/pup-rearing season (April-June) and prebreeding season (July-December) for all foxes;

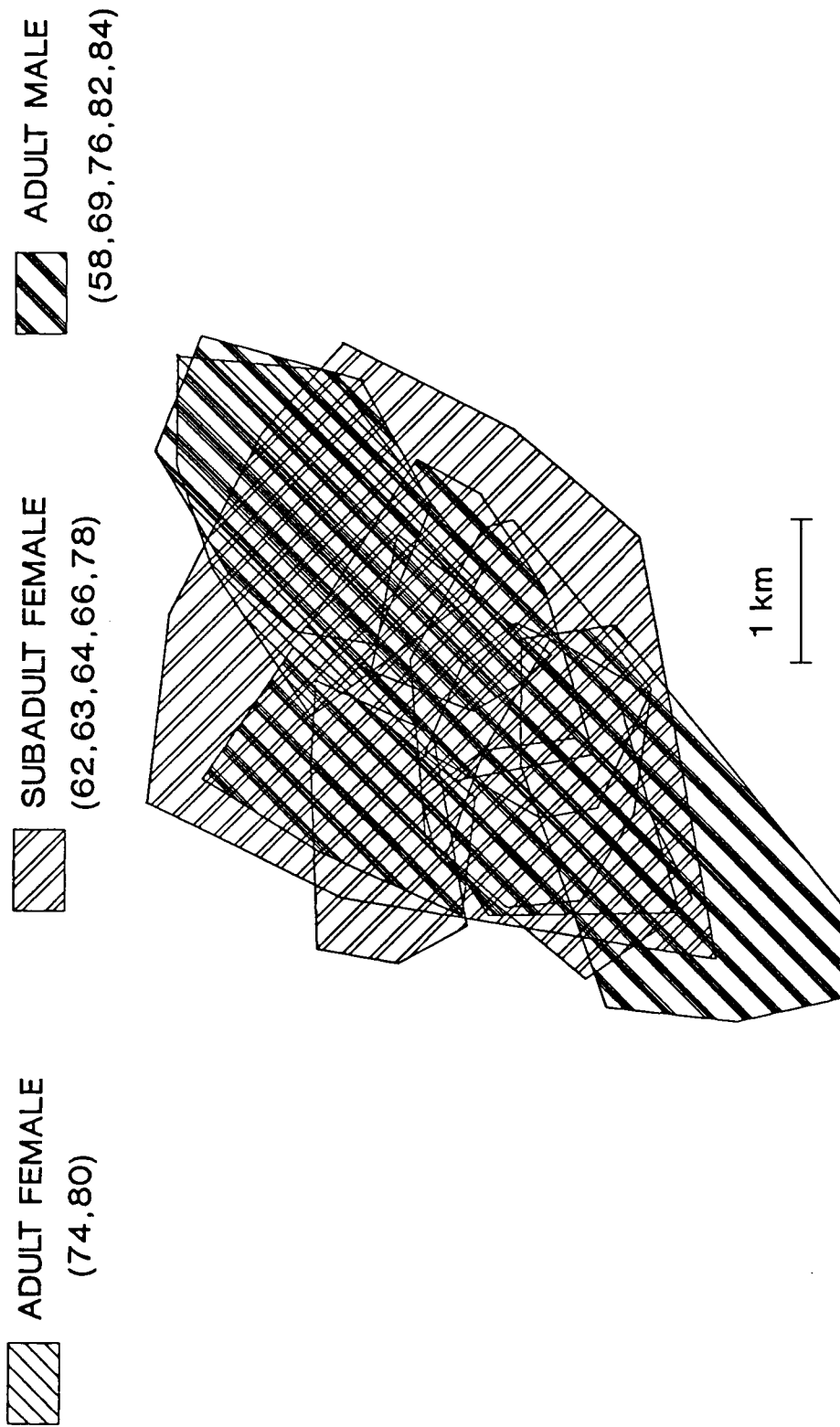


Figure III-1. Composite home ranges of 5 adult male, 2 adult and 5 subadult female gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

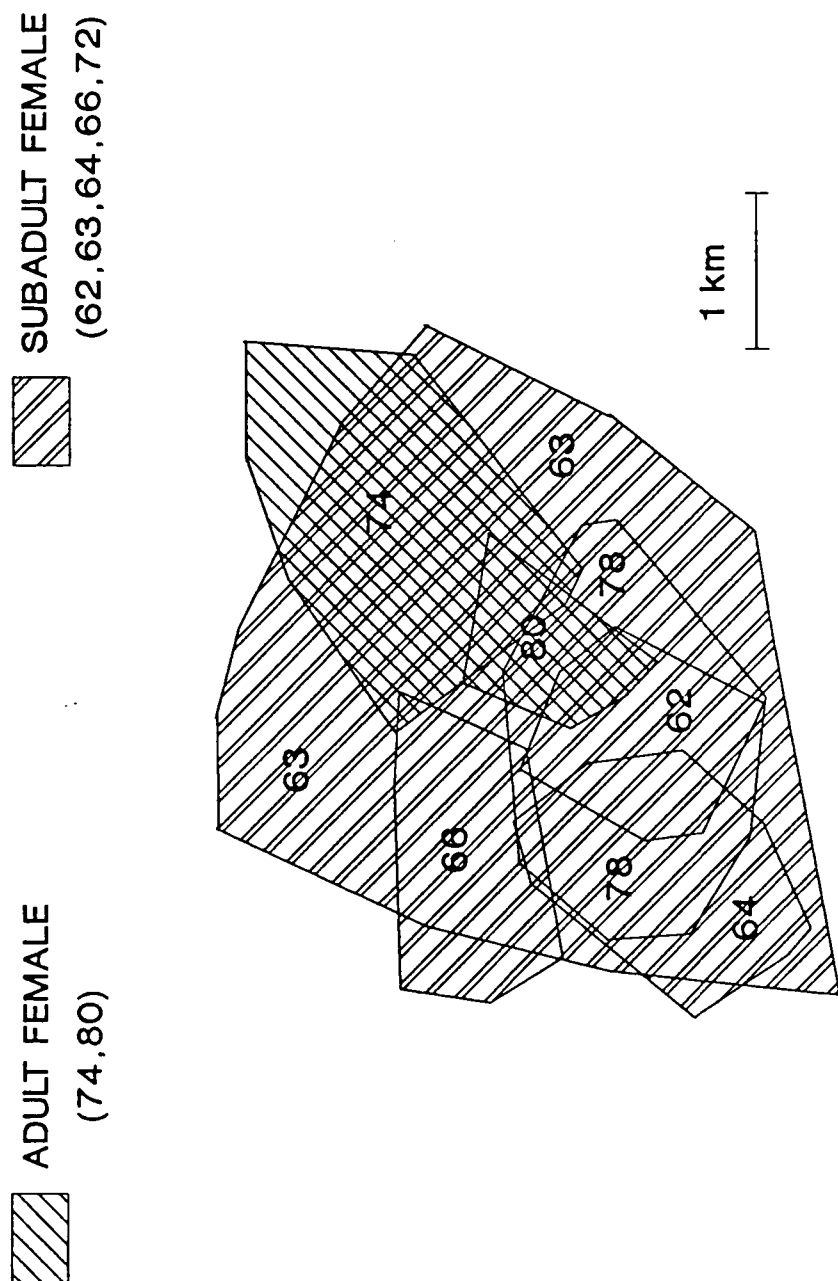


Figure III-2. Composite home ranges of 2 adult and 5 subadult female gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

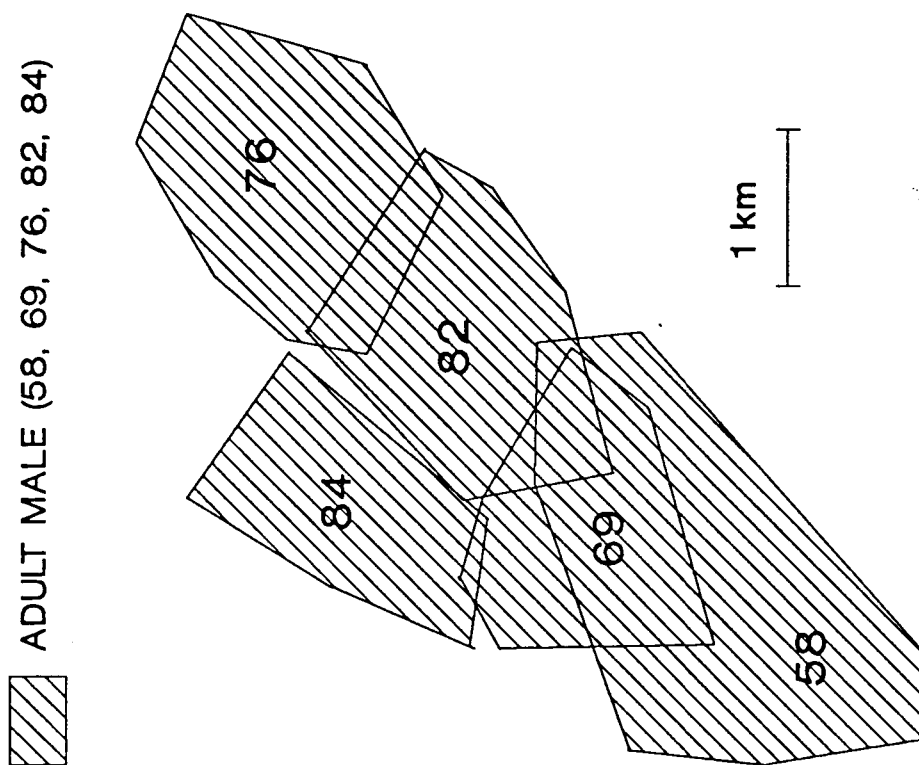


Figure III-3. Composite home ranges of 5 adult male gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

between males and females within each season ($p=0.79121$; $p=0.4210$; $p=0.6590$ respectively), or as an interaction between sex and breeding cycle ($p=0.2560$). This result was probably due to high variance between individual foxes, in combination with a small sample size. Changes in home range size among seasons for individual foxes was apparent, but did not appear to correspond to any obvious patterns. "Core areas", or areas of heavy use remained relatively constant between seasons (Figures III-4 to III-11).

Home range sizes for 12 gray foxes in 3 breeding seasons are summarized in Appendix, Table A-5 (see Figures III-4 to III-11 for illustration). Mean home range size for 10 foxes was 2.72 km^2 in breeding season (range= $1.92\text{-}3.57$); 2.32 km^2 in pup season (range= $0.82\text{-}4.02$) and 2.83 km^2 in prebreeding season (range= $1.57\text{-}5.37$). Mean home range size for 3 males in breeding season was 2.67 km^2 (range= $2.39\text{-}2.92 \text{ km}^2$); in pup-season 2.79 km^2 (range= $1.52\text{-}4.02$), and in prebreeding season 2.60 km^2 (range= $1.71\text{-}3.23$). For 4 females, mean home range size in breeding season was 2.77 km^2 (range= $1.92\text{-}3.57 \text{ km}^2$); in pup season 1.98 km^2 (range= $0.82\text{-}3.46 \text{ km}^2$), and in prebreeding season 3.01 km^2 (range= $1.57\text{-}5.37 \text{ km}^2$).

An overall trend toward smaller home range size during whelping/pup-raising season in females was apparent. Although no pups were observed, restricted movements and secure den sites dug into the roots of windthrown trees led to the suspicion that females 66 and 74, and her mate male 76 had pups. As presented in Appendix, Table A-5 (illustrated in Figures III-4 to III-11), their movements were restricted during whelping and pup-rearing season. Females 63, 78, and

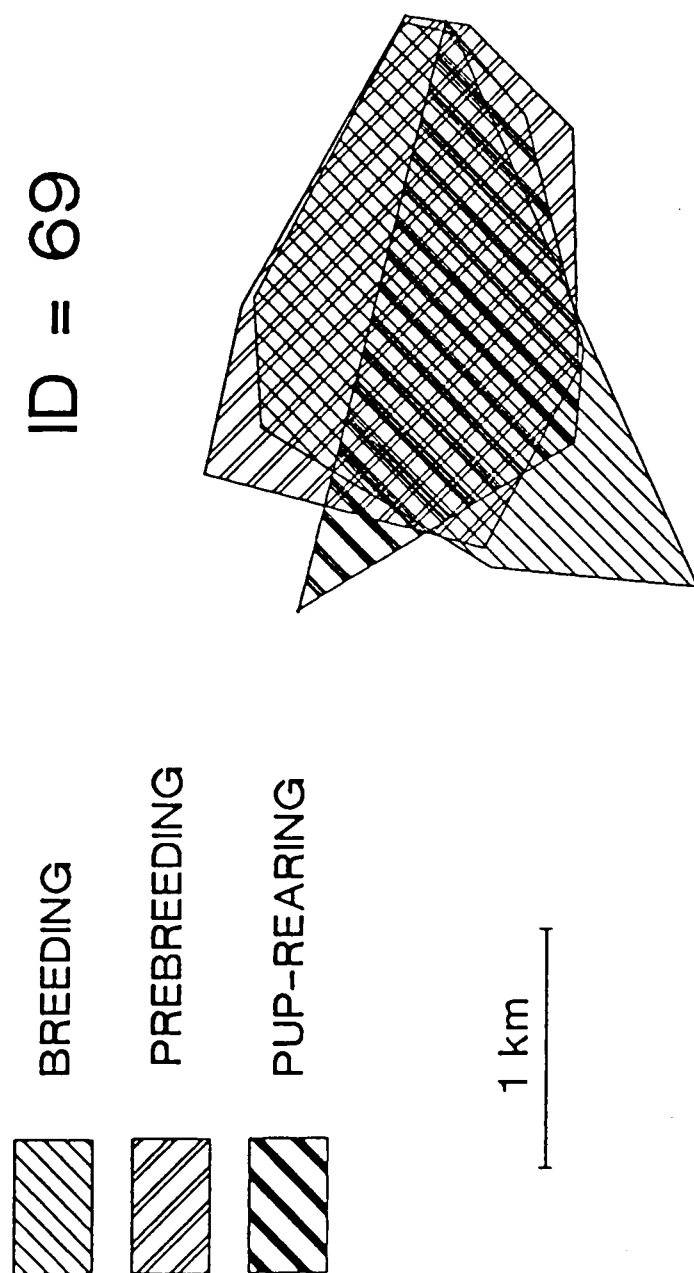


Figure III-4. Seasonal home range areas and "core area" (darkest shading) for adult male fox 69 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

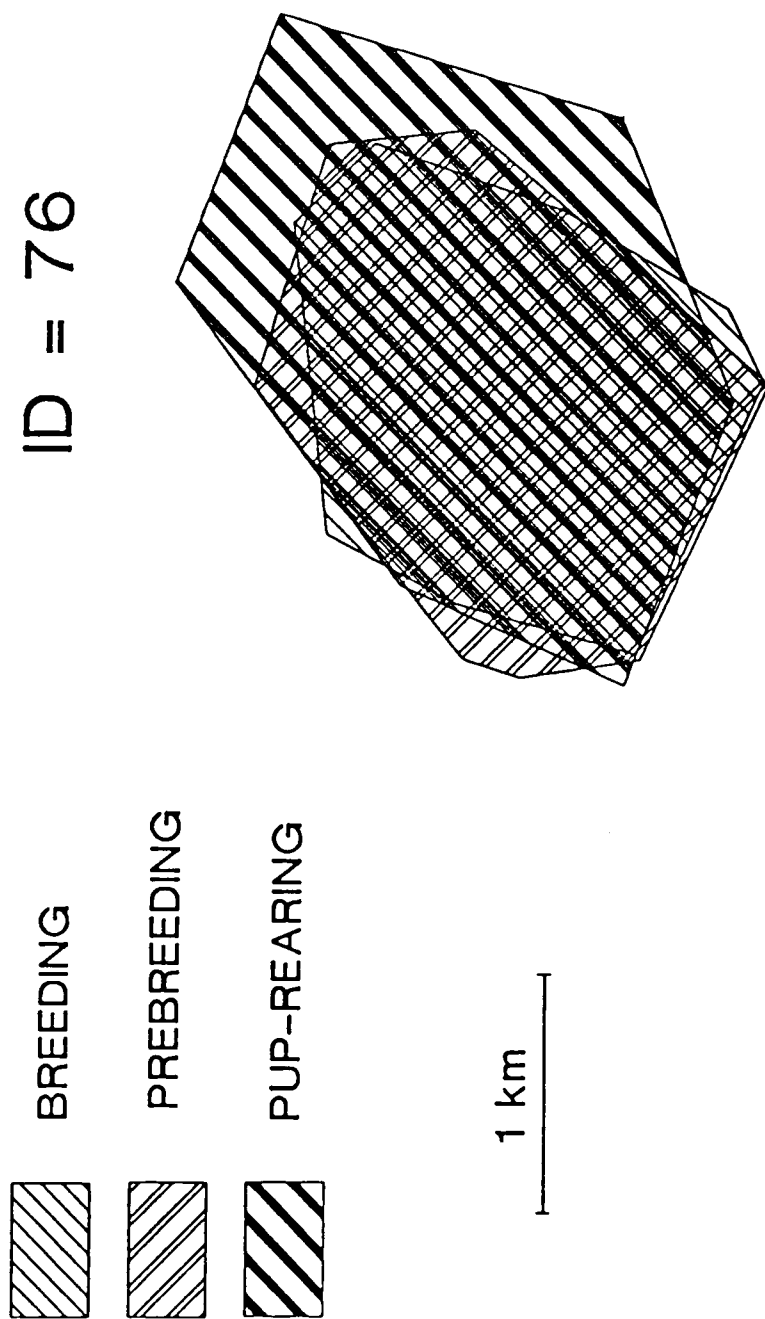


Figure III-5. Seasonal home range areas and "core area" (darkest shading) for adult male fox 76 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

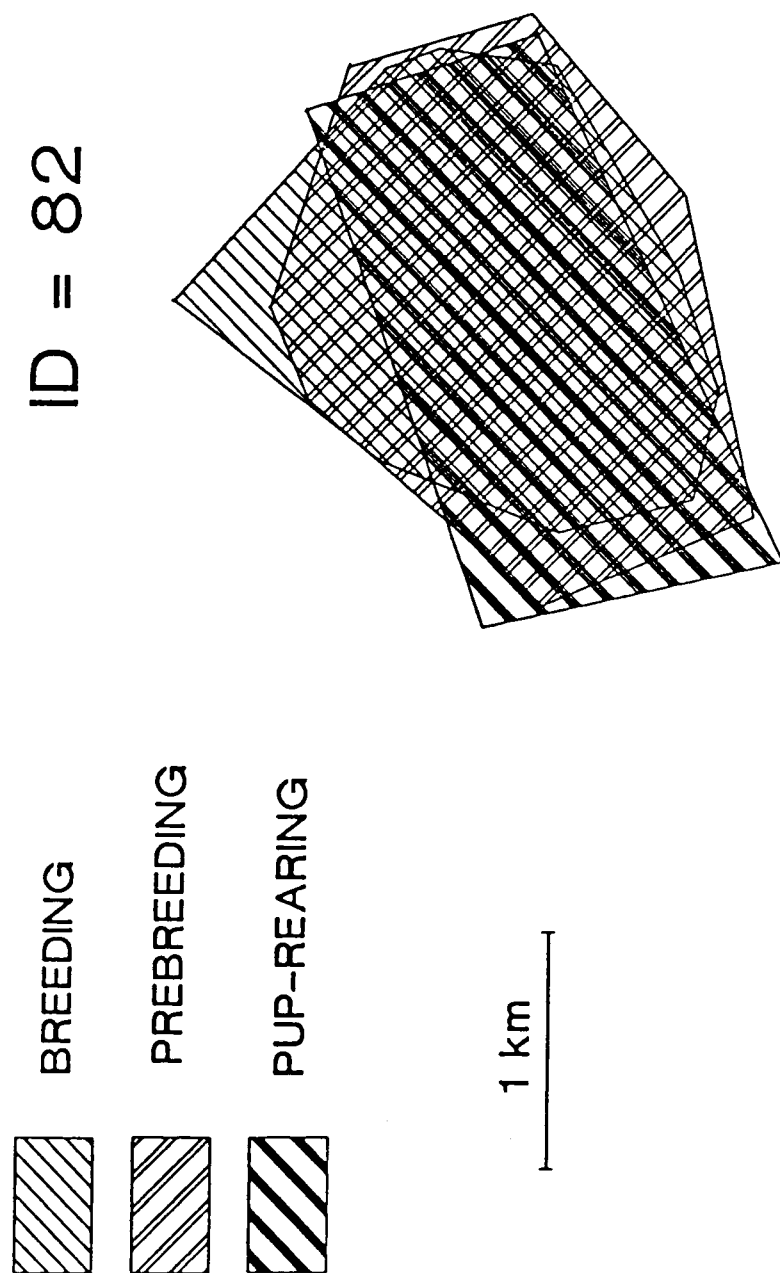


Figure III-6. Seasonal home range areas and "core area" (darkest shading) for adult male fox 82 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

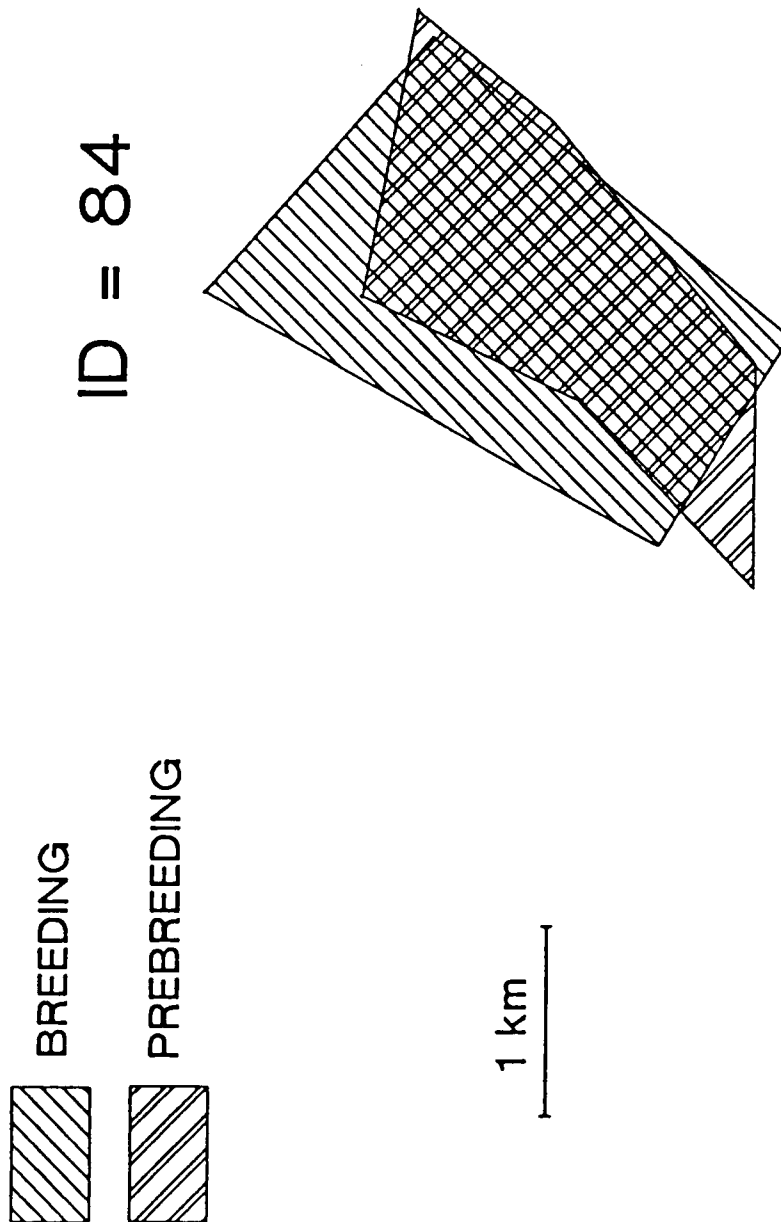


Figure III-7. Season home range areas and "core area" (darkest shading) for adult male fox 84 based on breeding (Jan.-Mar.) and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

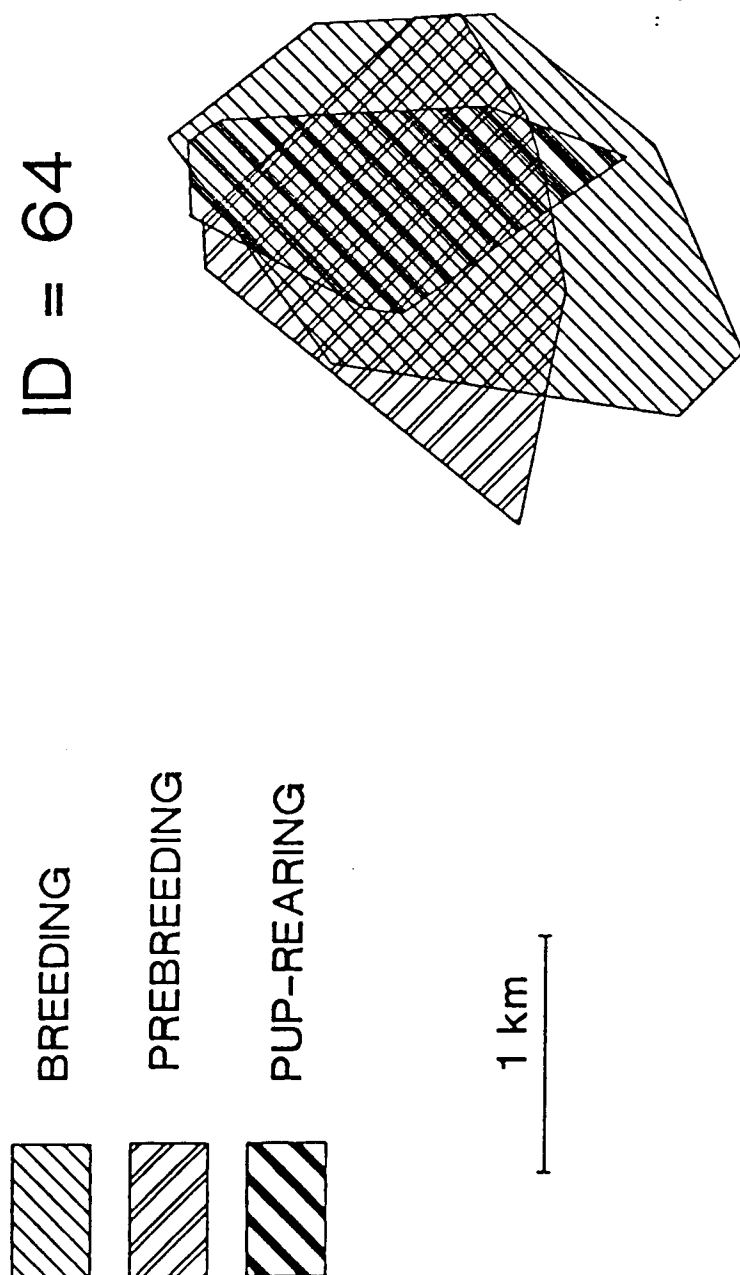


Figure III-8. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 64 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

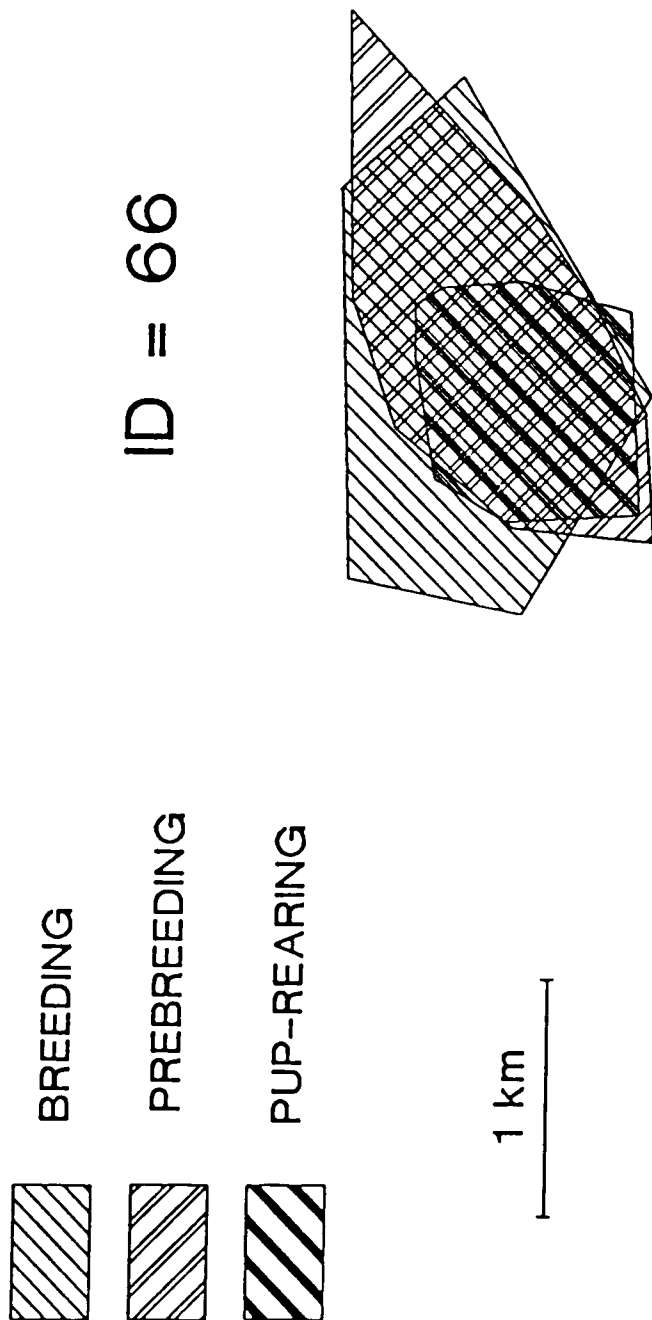


Figure III-9. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 66 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

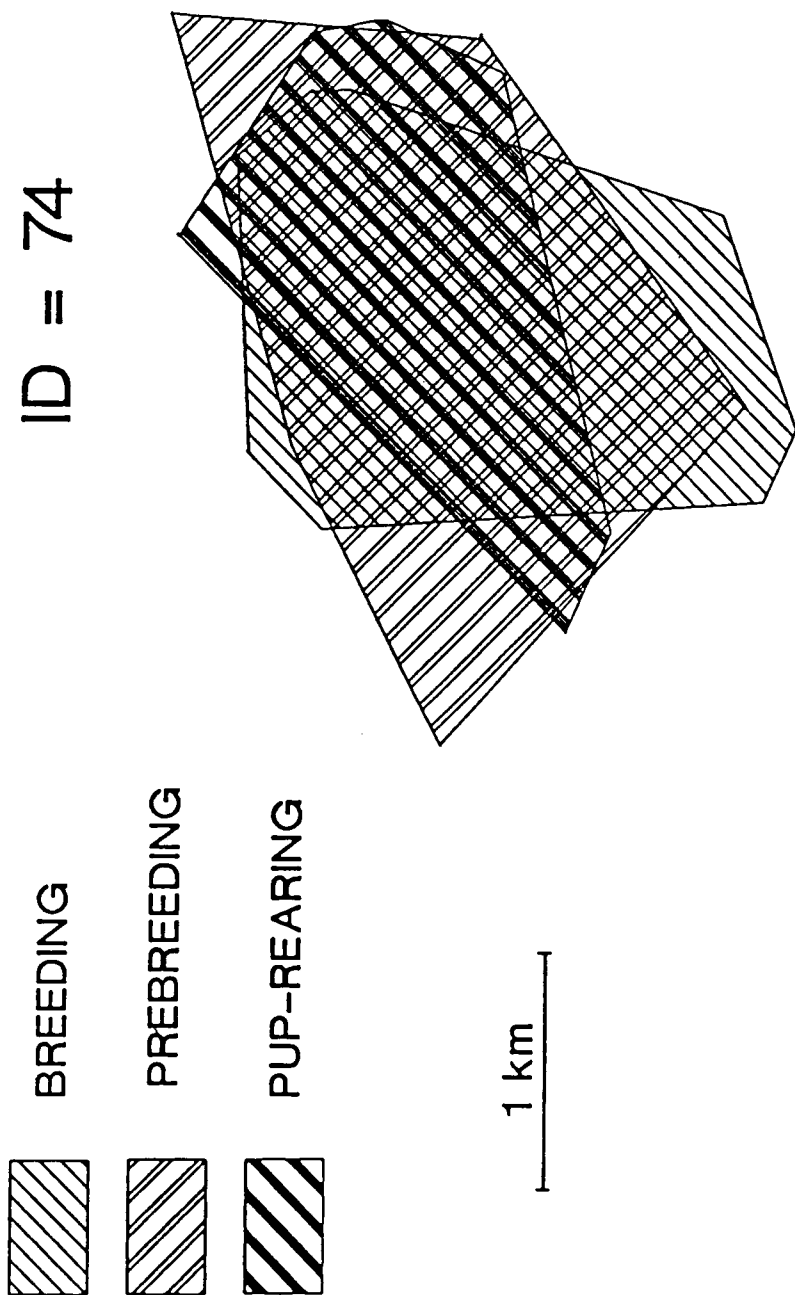


Figure III-10. Seasonal home range areas and "core area" (darkest shading) for adult female fox 74 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

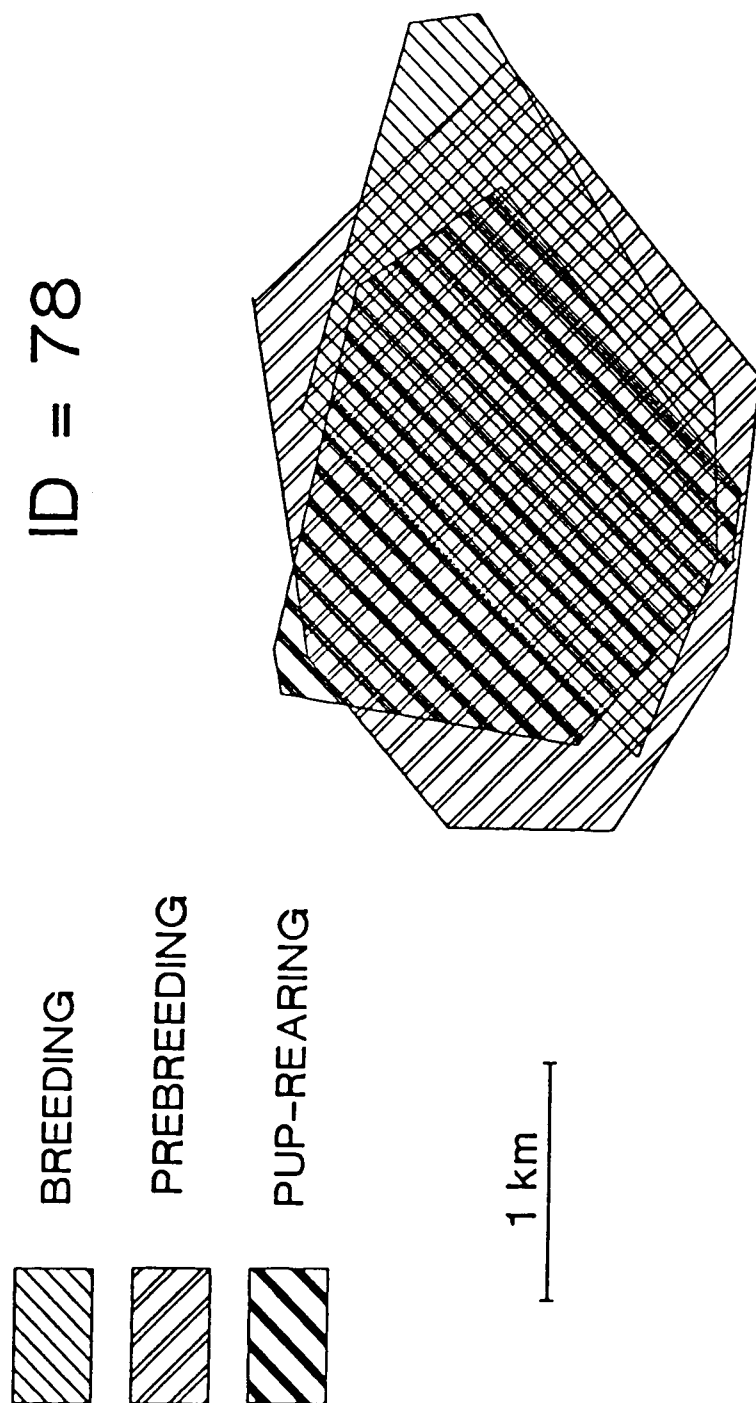


Figure III-11. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 78 based on breeding (Jan.-Mar.), pup-rearing (Apr.-July), and prebreeding (Aug.-Dec.) seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

64, however, were thought to be barren. Although 63 was in estrus (based on vulvar tumescence: Sheldon 1949) when trapped on 25 February 1987, her wide-ranging movements during whelping/pup-rearing season strongly indicated that she did not successfully whelp. Female 64 did exhibit a smaller home range size during whelping season, however, her death in May resulted in a small sample size for locations during this season, possibly resulting in an artificially small estimate of her home range size. She was not lactating when she was struck by a vehicle and killed on 12 May 1987. Female 78 exhibited a small reduction in home range size during breeding season, however, her seemingly unrestricted movements during whelping season led to the suspicion that she also did not have pups.

As discussed above, "sallies", or "atypical" movements of foxes (Ables 1968) were not included in home range estimates. It appeared more valid to treat some fox movements as erratic, exploratory movements rather than actual expansions of home range areas. Nonetheless, it is of interest to note that for all 3 foxes for whom locations were excluded, all "excursions" occurred in winter months. For subadult female fox 78, 2 known excursions occurred in December, with locations approximately 0.75 and 1.25 km east of the outer boundary of her "normal" composite home range. Two additional known excursions occurred in January, with locations approximately 0.75 and 2.5 km east and southeast of her "normal" home range boundaries, respectively. The latter location was verified; she was behind some office buildings. These excursions probably were too early to be associated with breeding season, but were more likely exploratory

movements for potential dispersal into a new home range area; no actual move occurred. Nicholson (1982) also noted that subadult females made excursions up to 3 km from their natal area, but always returned.

Of several excursions made by adult male fox 69, all occurred during February and March, and were probably associated with breeding activities. On 2 February, and during the weeks of 19 February-2 March, locations indicated that most excursions were between 1-1.8 km west of his "normal" home range boundary. On 12 January, and in the week of 19-22 February, 69 appeared to be exploring in an area between 1 and 1.5 km east of his normal home range boundary and within the known southwest portion of the home range of adult male gray fox 82. This was the only period during which he overlapped significantly with male fox 82. All known excursions by adult male fox 76 also occurred between 19-26 February, and again on 3 March. All excursions were between 0.5 and 1.5 km southwest of his normal home range boundaries, and also within adult male fox 82's home range (within the northeast portion). These excursions also were probably associated with breeding activities; this is of special interest, since 76 frequently travelled and rested with female fox 74 for the entire tracking period, indicating that the 2 were a bonded pair. Male fox 58 was not tracked for a sufficiently long time period to determine whether his 16 March 1987 capture and subsequent locations within the home ranges of 2 adult males (69 and 82) and subadult females (62, 78 and 64) were wanderings beyond his usual home range, or whether he lived within the home range of these radio-collared foxes. Since locations made in April were southwest of the home ranges of other study animals, it was suspected

that his presence in this area also were associated with breeding activities.

Thus, although variation between individual gray foxes may have obscured statistical detection of differences between males and females, trends suggested that differences in home range sizes and behavior within a breeding cycle and between sexes existed as explained by Follmann (1973). Males tended to roam further, entering the home ranges of other adult male gray foxes during breeding season only, while females did not exhibit this tendency. MacDonald (1980) also noted this tendency in male red foxes. Female (especially those who were suspected of bearing offspring) home range sizes were generally observed to become smaller in whelping/pup-rearing season (April-July) than in breeding or prebreeding season. This trend was not as pronounced in males.

An ANOVA revealed no significant differences in gray fox home range size ($n=10$) between "scarce food" (January-April) and "abundant food" (May-December) seasons ($p=0.3085$) for all foxes, nor between seasons as a function of sex (interaction) ($p=0.4041$). No significant differences in home range size between sexes were detected in either season alone ($p=0.4847$ and $p=0.8115$, respectively). These results were probably due to such high variance between individual foxes, in combination with small sample sizes. Differences in home range size among seasons for individual foxes was apparent, but did not appear to correspond with any obvious patterns, nor the influence of relative food abundance. "Core areas", or areas of heavy use remained relatively constant between seasons (Figures III-12 to III-19).

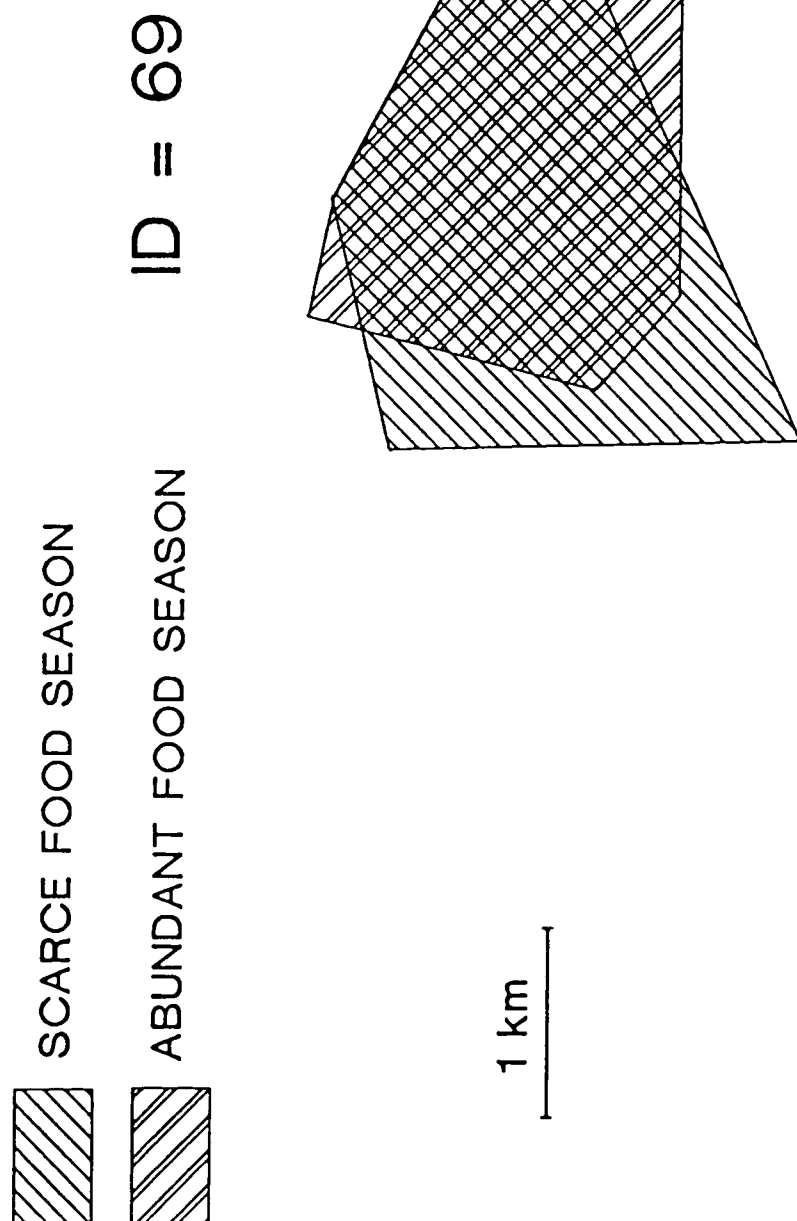


Figure III-12. Seasonal home range areas and "core area" (darkest shading) for adult male fox 69 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

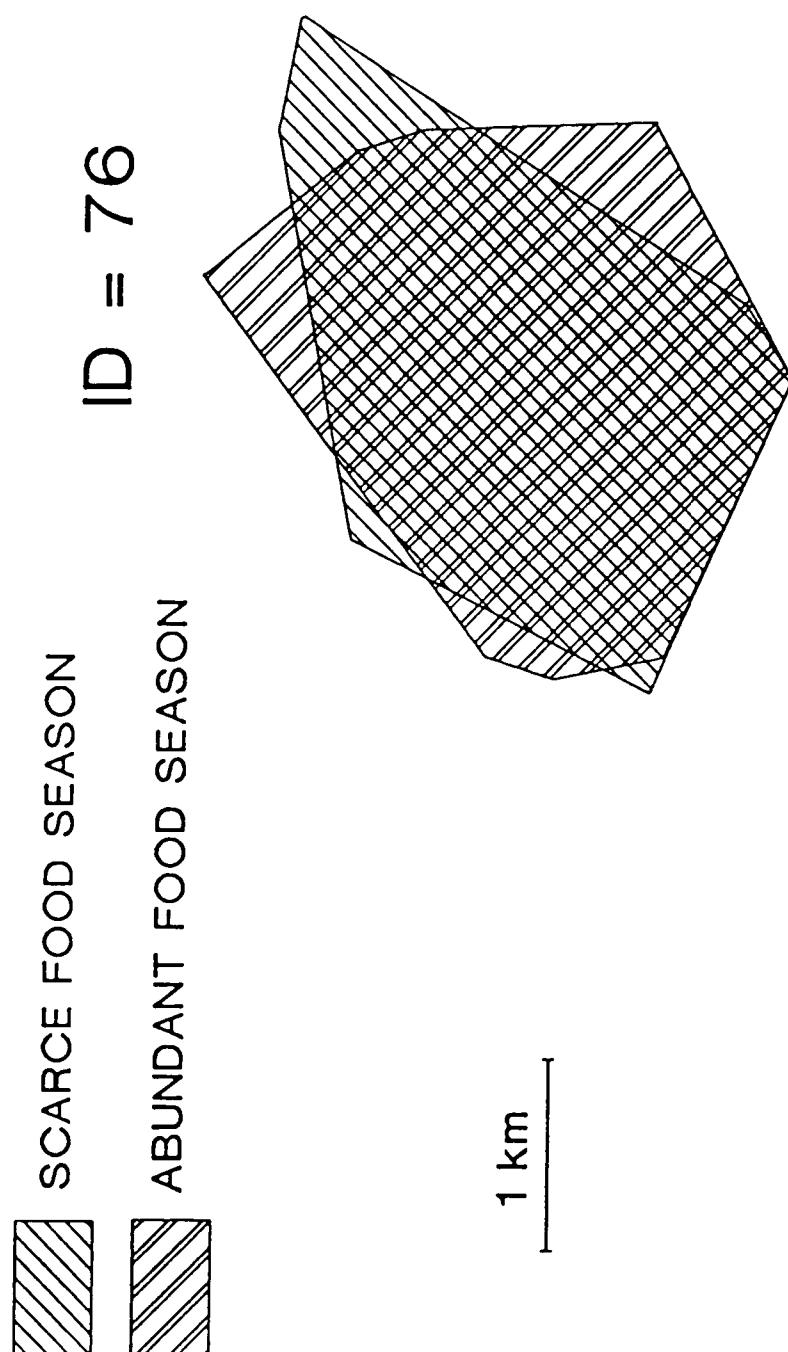


Figure III-13. Seasonal home range areas and "core area" (darkest shading) for adult male fox 76 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

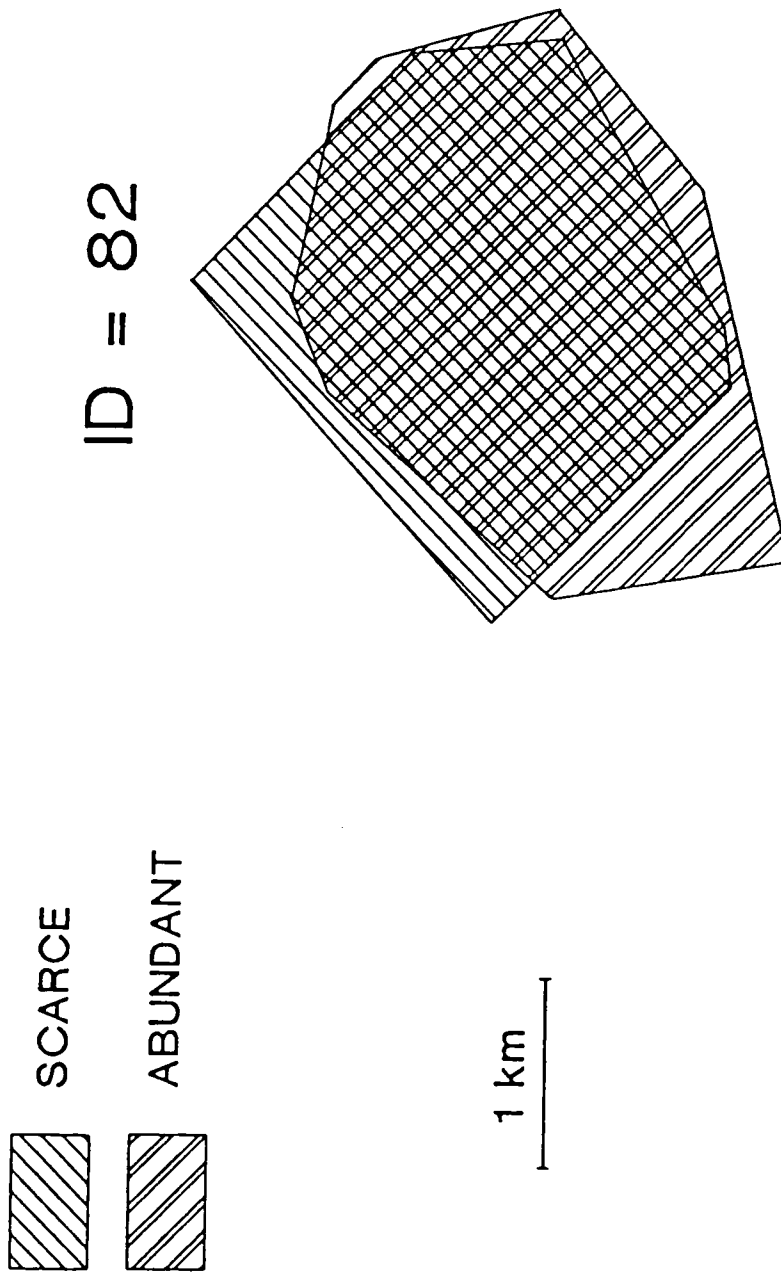
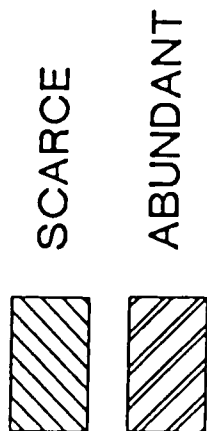
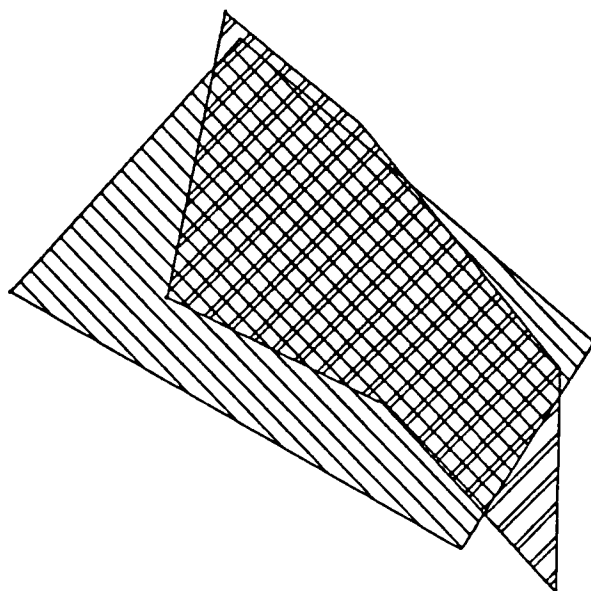


Figure III-14. Seasonal home range areas and "core area" (darkest shading) for adult male fox 82 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.



ID = 84



1 km

Figure III-15. Seasonal home range areas and "core area" (darkest shading) for adult male fox 84 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

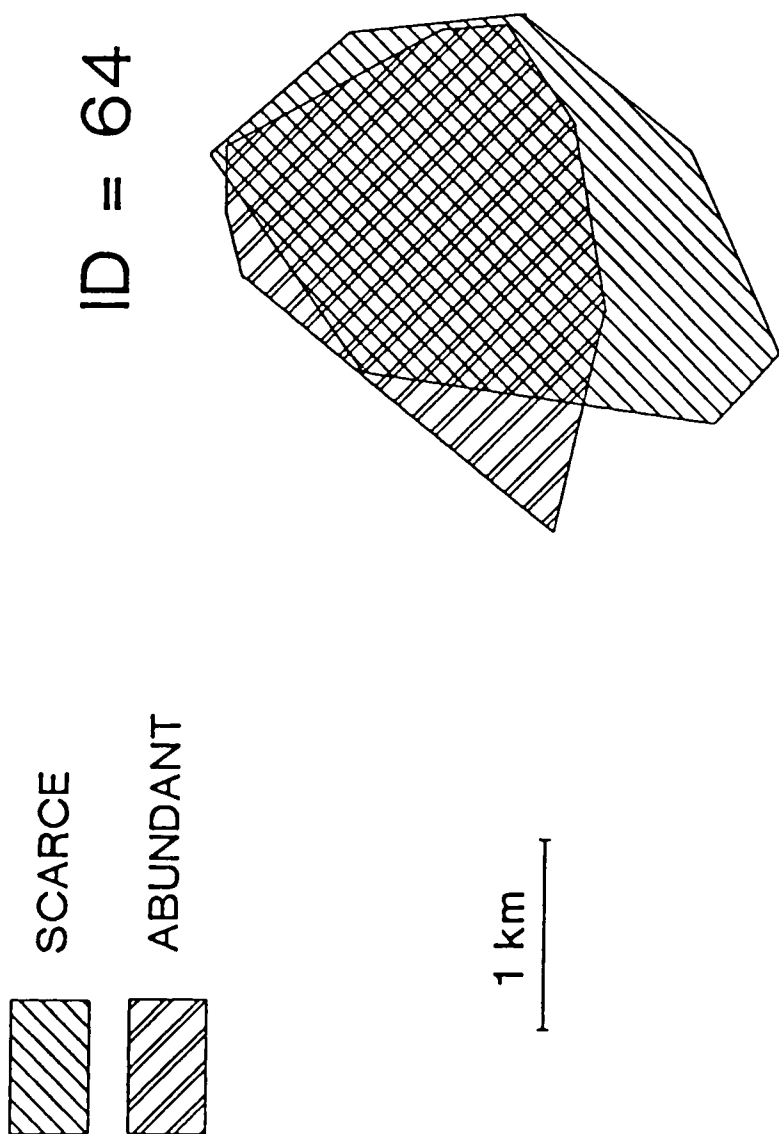
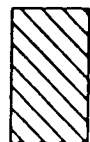
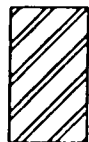


Figure III-16. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 64 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.



SCARCE



ABUNDANT

ID = 66

1 km

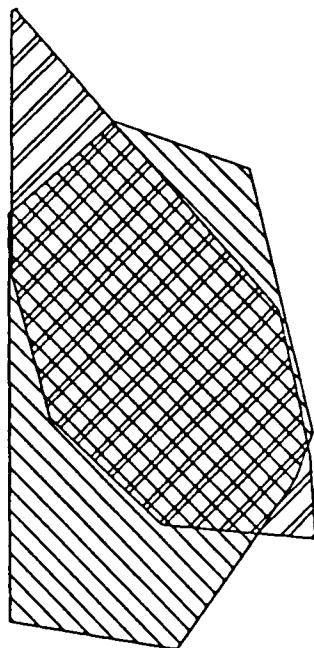


Figure III-17. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 66 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

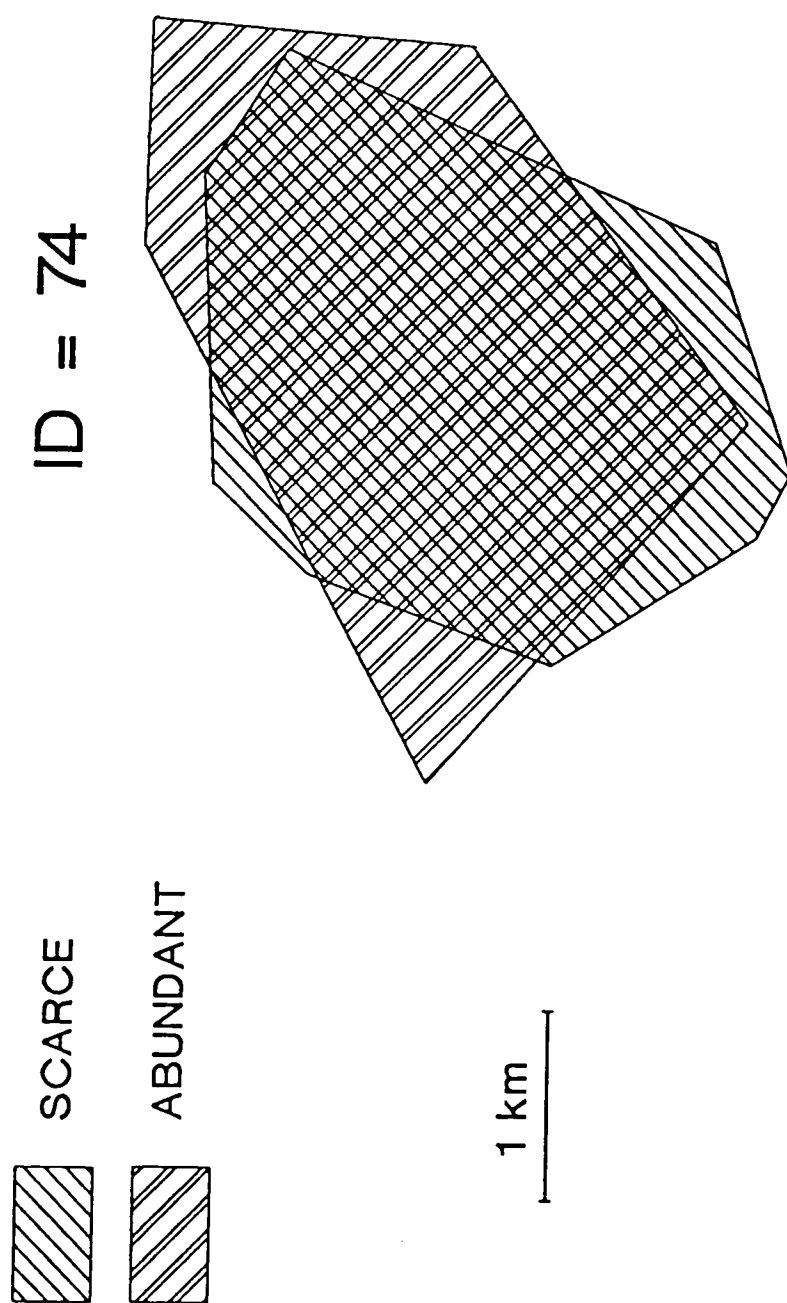


Figure III-18. Seasonal home range areas and "core area" (darkest shading) for adult female fox 74 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

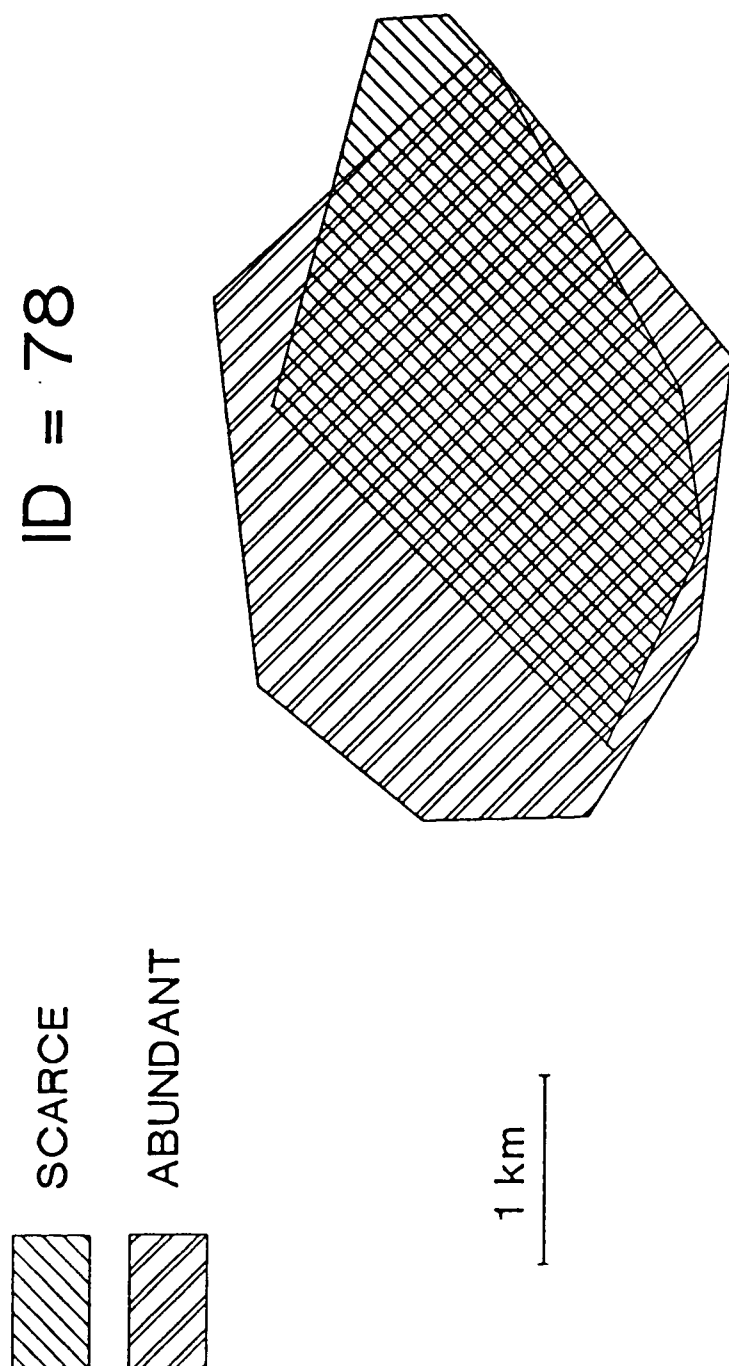


Figure III-19. Seasonal home range areas and "core area" (darkest shading) for subadult female fox 78 based on "abundant" (May-Dec.) and "scarce" (Jan.-Apr.) food seasons on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

Home range sizes for 12 gray foxes in 2 seasons of food abundance ("scarce" and "abundant" food) are summarized in Appendix, Table A-6 (illustrated in Figures III-12 to III-19). Mean home range size for 10 foxes during "scarce food" season was 3.43 km^2 (range=1.62-4.75); mean home range size during "abundant food" season was 2.92 km^2 (range=2.20-6.91). Mean home range for males was 3.75 km^2 in "scarce" food season, and 2.80 km^2 in "abundant" food season; mean home range size for females was 3.03 km^2 in scarce food season, and 3.01 km^2 in abundant food season.

The null hypothesis that an increase in food availability (or a dietary switch to the primary trophic level) had no influence on home range size in gray foxes was not refuted in this study. While several gray foxes exhibited an expansion in home range size during winter (January-April), when a switch to animal prey (presumably with a sparser density than the spring-summer-fall fruit and insect prey) might have necessitated a greater area for searching, several foxes exhibited the opposite trend (Table A-6; Figures III-12 to III-19). Since food supply, availability and heterogeneity of habitat, as well as population density were similar between areas utilized by radio-collared gray foxes, this disparity could not be attributed to differences in habitat quality or availability (Fuller 1978).

Resources other than food may have influenced home range variation between seasons. This is evidenced by similarity in home range size for males and females during "abundant" food season, but larger home ranges for males during "scarce" food season (January-April). These dates also encompass dates for breeding season, indicating that, in

general, males may range farther than females during breeding season. Excursions by males during the height of breeding season further emphasized the influence of biological factors in home range size.

Trapping effort was intense in September and early October, so that most of the foxes within the study area were thought to be radio-collared. However, all explanations offered for territoriality and population density must be considered tentative, since it is entirely possible that other unmonitored foxes lived within the area.

Composite home range boundaries suggested two likely explanations for gray fox distribution. First, male gray foxes may be somewhat territorial (Figure III-3), while females are not (Figure III-2). Alternatively, adult males and females are both somewhat territorial, sharing home ranges as pairs, while subadult foxes or family aggregations share home ranges and are not territorial with one another (Figure III-1). Very little overlap between adjacent home ranges was observed for the 4 males monitored intensively between September, 1986 and August, 1987. Overlap which did occur between 2 males was at peripheries rarely used by one. As discussed previously, excursions by male 69 and male 76 into 82's home range were observed in February and March, and were probably associated with breeding season. Fox 58 was not monitored long enough to ascertain whether any overlap occurred between his home range and other male home ranges except during breeding season, but before his radio-transmitter failed he appeared to concentrate his movements in the southwest portion of his range, not overlapping with other radio-collared foxes. Evidence for

territoriality for gray foxes has been reported in several other studies (Trapp 1978; Follmann 1973; Lord 1961).

Home ranges for subadult female foxes 64, 62, and 78 overlapped considerably, and were mostly contained within adult male 69's home range until 62 was killed (by predation, apparently) in January, and 64 was killed by a vehicle in May. Since these females were subadult, two explanations for such overlap are likely: first, that female gray foxes may be less territorial than males; secondly, that these foxes were all within a family group.

Judging by trapping and recapture data, Lord (1961) suggested that gray fox "family aggregations" appeared to be spatially segregated from other family units. Trapp's (1978) data suggested that this occurred in his study, with the home ranges of 3 female and 1 subadult male gray foxes coinciding with one or the other home ranges of 2 adult male foxes (Trapp and Hallberg 1975). This explanation is further supported by the observation that foxes 64 and 62 frequently used the same daytime resting place on different days (in thick brambles and brush along a powerline); they, along with 69 and 78 were frequently very close to one another along or adjacent to this powerline on the same day.

Other female gray foxes did not exhibit overlap with other females, but did coincide each with one male fox. Adult female 74 and adult male 76 shared virtually the same home range, apparently to the exclusion of other foxes. This pair travelled and rested together frequently, and during denning season were both frequently in the vicinity of the den; they were presumed to be a mated pair. Adult

female 80 and adult male 82 were trapped at the same location 2 nights apart. Fox 80's home range was contained entirely within 82's home range, and the two were located resting together on a few occasions. Unfortunately, 80 died before enough observations were made to determine an unbiased home range size and shape, or, with some degree of certainty, whether these two were a mated pair. It was suspected that they were, however due to the above observations. Subadult female 66 and adult male 84 also shared a home range to the apparent exclusion of other foxes. This may have been part of a "family aggregation" as well, however, judging by difference in maturity between the 2 foxes. Subadult female 63 was located within the home range of all radio-collared gray foxes at one time or another during the time she was tracked (25 February-1 September 1987). She did not remain in any one area for any length of time, however, and her atypical ranging behavior makes it unlikely that these locations should be considered "overlap", or "home" range at all.

Where sex alone is considered then, this study indicates that male gray foxes are territorial, while females may not be as strongly so. However, when age is also accounted for, the more likely explanation for gray fox home range distribution and overlap becomes one of relatively exclusive territories shared between one adult male and female pair, and possibly their (yearling) offspring.

Although home range size was not constant for individual foxes among seasons in the present study, it appeared that adult foxes recognized the boundaries of neighboring fox's "composite" home ranges year-round, which therefore remained relatively exclusive for pairs or

family aggregations (Figures III-1 to III-3). "Core areas" remained relatively constant between seasons (Figures III-4 to III-19).

Although territorial defense could not be established in the current study, scats were often observed in prominent locations, such as along roads and at road intersections, often in piles of 2 or 3. This may have been indicative of "defense" by scent-marking, and has also been observed in several other studies on gray foxes (e.g. Trapp 1978; Richards and Hine 1953; Grinnell et al. 1937; Wood et al. 1958).

It has been suggested that territoriality may not be necessary for survival or reproductive success (fitness) where resources are abundant (Davies 1978; Ewer 1973; Kaufmann 1983; Jonkel and Cowan 1971). In the present study, resources may be seasonally abundant (summer and fall fruits), but also seasonally scarce (winter animal prey). MacDonald (1980; 1983) suggested that a territory must be large enough, and contain sufficient resources to support at least a pair of foxes from year to year, while additional foxes might be accommodated within that area in times of sufficiently abundant food. The dispersion of resources then, may influence the size and shape of territories, since patches may temporally vary in their food production, and since a minimum amount of food must be contained within the boundaries. The "evolutionarily sound strategy" (ESS) of maintaining defined territories rather than vague home ranges in winter food-limited areas is evident.

Nothing regarding territoriality or determinants of home range (or territory) size may be conclusively stated based on the small sample size and variability between individuals observed in the present study,

as well as the lack of controlled experiments or comparison of studies under contrasting environmental conditions. It is suggested nonetheless that von Schantz's (1984b) argument that "the animal's territory sizes will be so adjusted that they contain enough food for reproduction, or at least survival, during the bottle-neck years (or, in this case, the winter season as well) of food scarcity" is of relevance in the study of gray foxes, at least in areas of seasonal food limitation.

Density and Mortality

Using home range data, population estimates were made for adult gray foxes on the ORR. With a mean home range size for adult gray foxes estimated at 4.41 km^2 , and assuming that an adult male and female share a home range (Trapp and Hallberg 1975; also based on observations in the current study), a conservative spring estimate (post-dispersal and pre-birth) of 0.45 adult gray foxes per km^2 was calculated. A post-birth estimate, given an average of 4 young born per mated pair (Wood 1958; Richards and Hine 1953; Sheldon 1949; Sullivan 1956; Layne 1958), might reach as high as 1.36 foxes/km^2 . This density estimate was low relative to several studies (reported densities range from 0.38 in California chaparral (Grinnell et al. 1937) to 10.38 km^2 in southern Wisconsin (Errington 1933), a somewhat surprising finding, given the protected status of the ORR and apparent prime gray fox habitat conditions. A low density however, corresponds with the relatively larger home range sizes for gray foxes in the present study, as predicted by Clutton-Brock and Harvey (1979).

Annual gray fox mortality (Appendix, Figure A-1) in the current study was at least 38% for all ages combined. Mortality rate was 50% for subadult (3 of 6 subadults died), and 28% for adult gray foxes. Of 13 radio-collared foxes, one old female died of apparently natural causes (unknown); one subadult male died of apparently trap-related injuries (he was not included in any statistical calculations, since he was not monitored for an adequate length of time to gather valid data); one adult male and one subadult female were killed by vehicles, and one subadult female was apparently preyed upon, possibly by a bobcat. The fate of 2 adult male foxes was unknown due to radio-transmitter failure before the end of the study. These mortality rates were low compared to most studies, however these data may not accurately reflect mortality. Subadult foxes were trapped in the fall, well after the most vulnerable first few months of their lives (Lord 1961; Wood 1958). Sample size was probably insufficient for accurate estimates as well. Prohibition of trapping from the ORR might have some impact on low mortality rates, although human impact on gray fox mortality was not absent, as was evidenced by vehicle-related mortalities.

SUMMARY AND CONCLUSIONS

The null hypotheses that no differences in home range size for gray foxes existed between males and females, among breeding, whelping/pup-raising, and prebreeding season, or between seasons of high and low food availability were not refuted by statistical analyses. Differences in seasonal home range size for individual foxes was

apparent, but did not correspond to any obvious pattern or influence. Average composite home range size was 3.97 km^2 for 10 foxes (4.41 km^2 for 6 adults, and 3.32 km^2 for 4 subadults). Territoriality was suggested by the spatial distribution of adult foxes in the present study. Home ranges appeared to be coincident between adult male and female pairs, and between subadult and adult gray foxes within a presumed "family aggregation", but little overlap occurred between adult male or adult female foxes. The density for adults was estimated at 0.45 per km^2 , a low estimate relative to most other studies reporting densities.

Several studies on gray foxes have suggested that a relationship between home range size and environmental/biological factors exist (e.g. Nicholson 1982; Follmann 1973), but fail to statistically demonstrate their conclusions. In the above studies, as for the present study, problems involved in accurate statistical demonstration of such relationships, should they exist, include small sample size and high variation in home range size between individual foxes.

Differences in male and female behavior during breeding and whelping seasons as observed in the present study and others might legitimately lead to the conclusion that biological factors influence home range size in gray foxes. Evidence for a strong environmental influence on seasonal home range sizes however, is sketchier.

The positive relationship between the amount of flesh (or relative food density) in an animals diet and home range size has been demonstrated by interspecies comparisons (Schoener 1968; McNab 1963; Gittleman and Harvey; Harestad and Bunnell 1979). The present study

suggested that this relationship may not exist for gray foxes in east Tennessee as they switch dietary trophic level with seasonal changes in food availability. MacDonald (1980; 1983) noticed that territory sizes in red foxes did not change on a year to year basis, but each contained a sufficient quantity of resource "patches" to provide for year-round food requirements.

Individual home range sizes changed (seemingly randomly) among seasons, but "core areas" within home ranges appeared to remain relatively constant (Figures III-4 to III-19). Although no conclusive statements may be made based on such a small sample size and high individual variability, the findings of the present study suggest, in agreement with MacDonald (1980, 1983), that environmental factors (food availability) may have influenced the establishment of territories, within which were contained sufficient resources for periods of food scarcity (in this case winter) as well as periods of plenty. Seasonal changes in home range areas to correspond with changes in dietary trophic level were therefore not necessary to obtain sufficient resources.

It has been suggested that territorial behavior corresponds somewhat to scarcity of defensible resources (e.g. Jonkel and Cowan 1971; Ewer 1973; Brown 1975). In such cases (e.g. some geographical regions and/or seasonal resource scarcity), territoriality may be necessitated to better insure reproductive fitness in the "worst case scenario". Territorial defense of an area which contains a "known" adequate year-round resource base may be a better individual strategy

than the uncertainty involved in continual fluctuation of home range size in response to environmental variables.

The question of what influences home range or territory size was not conclusively determined in the present study. Nonetheless, some general rules are hypothesized. If, due to time and energy costs, animals defend only the minimum area required to provide adequate resources (in this case food) (Mace et al. 1983), the upper limit of gray fox home range size in east Tennessee may be determined by winter food availability, when presumably (animal) prey is dispersed more widely than spring, summer, and fall food sources (insects and fruit). Although no significant differences in home range size were observed among seasons of frugivorous, insectivorous, or carnivorous food habits, the catholicity of gray fox food habits may enable the species to have relatively smaller territory sizes than similar-sized carnivores with diets of a higher flesh-content. A relatively low density however, may have "permitted" larger territories than an area saturated with gray foxes. Yet, lean winters with relatively sparser prey density may have in turn limited the gray fox population. It has been suggested (MacDonald 1983) that periods of low food availability may ultimately determine territory sizes. While "low food availability" normally corresponds to winter in east Tennessee, when foxes must rely on animal foods, it is further suggested that within a given area, the primary and ultimate determinant of territory size may be the highest trophic level on which a given species relies for any length of time, and only secondarily on the dispersion of those resources.

LITERATURE CITED

- Ables, E.D. 1968. Ecological studies on red foxes in southern Wisconsin. PhD dissertation, Univ. of Wisconsin. 132pp.
- Andelt, W.F., and P.S. Gipson. 1979. Home range, activity and daily movements of coyotes. *J. Wildl. Manage.* 43:944-951.
- Bekoff, M., and L.D. Mech. 1984. Computer simulation: simulation analyses of space use: home range estimates, variability, and sample size. *Behav. Res. Meth., Instr., and Comp.* 16:32-37.
- Bowen, W.D. 1982. Home range and spatial organization of coyotes in Jasper National Park, Alberta. *J. Wildl. Manage.* 46:201-215.
- Boyle, K.A. 1986. A comparison of methods of home range analysis. M.S. thesis, Clemson Univ. 67pp.
- Brand, C.J., L.B. Keith, and C.A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. *J. Wildl. Manage.* 40:416-428.
- Brown, J.L. 1975. The evolution of behaviour. W.W. Norton, N.Y. 761pp.
- Brown, J.L., and G.H. Orians. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* 1:239-262.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24:346-352.
- Clutton-Brock, T.H., and P.H. Harvey. 1979. Home range size, population density and phylogeny in primates. Pages 201-214 in Bernstein, I.S., and E.O. Smith, eds. *Primate ecology and human origins.* Garland Publishing, Inc., N.Y.
- Davies, N.B. 1978. Ecological questions about territorial behavior. Pages 317-350 in Krebs, J.R., and N.B. Davies, eds. *Behavioural ecology: an evolutionary approach.* Blackwell Scientific Publications, Oxford.
- Dunn, J.E. 1977. Optimal sampling in radio telemetry studies of home range. Univ. of Arkansas Statistics Lab. Tech. Rept. No. 5:53-70.
- Errington, P.L. 1933. Bobwhite winter survival in an area heavily populated with gray foxes. *Iowa State Coll. J. of Sci.* 8:127-130.
- Ewer, R.F. 1973. The carnivores. Comstock Pub. Assoc., Cornell Univ. Press, Ithaca. 494pp.

- Follmann, E.H. 1973. Comparative ecology and behavior of red and gray foxes. PhD thesis, Southern Ill. Univ., Carbondale. 152pp.
- Fuller, T.K. 1978. Variable home-range sizes of female gray foxes. *J. Mammal.* 59:446-449.
- Garshelis, D.L. 1983. The role of sampling intensity in the selection of a home range model. Pages 270-275 in Pincock, D.G., ed. *Proc. 4th Internat. Conf. on Wildl. Biotelem.*
- Gier, H.T. 1948. Rabies in the wild. *J. Wildl. Manage.* 12:142-153.
- Gittleman, J.L., and P.H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.* 10:57-63.
- Grinnell, J., J. Dixon, and J.M. Linsdale. 1937. Fur-bearing mammals of California. Vol. II. Univ. of California Press, Berkeley. Pages 377-777.
- Hallberg, D.L., and G.R. Trapp. 1984. Gray fox temporal and spatial activity in a riparian agricultural zone in California's central valley. Pages 920-928 in Warner, R.E., and K.M. Hendrix eds. *California riparian systems: ecology, conservation and productive management.* University of California Press, Berkeley.
- Harestad, A.S., and F.L. Bunnell. 1979. Home range and body weight - a reevaluation. *Ecology* 60:389-402.
- Haroldson, K.J., and Fritzell. 1984. Home ranges, activity, and habitat use by gray foxes in an oak-hickory forest. *J. Wildl. Manage.* 48:222-227.
- Harvey, P.H., and G.M. Mace. 1982. Comparisons between taxa and adaptive trends. Pages 343-361 in King's College Sociobiology Group: *Current problems in sociobiology.* Cambridge University Press, Cambridge.
- Heezen, K.L., and J.R. Tester. 1967. Evaluation of radio-tracking by triangulation with special reference to deer movements. *J. Wildl. Manage.* 31:124-141.
- Hersteinsson, P., and D.W. MacDonald. 1982. Some comparisons between red and arctic foxes, *Vulpes vulpes* and *Alopex lagopus*, as revealed by radio-tracking. *Symp. Zool. Soc. Lond.* 49:259-289.
- Jonkel, C.J., and I. McT. Cowan. 1971. The black bear in the spruce pine forest. *Wildl. Monogr.* 27:5-57.
- Kleiman, D.G., and J.F. Eisenberg. 1973. Comparisons of canids and felid social systems from an evolutionary perspective. *Anim. Behav.* 21:637-659.

- Kaufmann, J.H. 1983. On the definitions and functions of dominance and territoriality. *Biol. Rev.* 58:1-20.
- Kruuk, H., and T. Parish. 1982. Factors affecting population density, group size and territory size of the European badger (Meles meles). *J. Zool. Lond.* 196:31-39.
- Lack, D. 1966. Population studies of birds. Oxford Univ. Press. 341pp.
- Laundr e J.H., and B.L. Keller. 1984. Home range size of coyotes: a critical review. *J. Wildl. Manage.* 48:127-139.
- Layne, J.N. 1958. Reproductive characteristics of the gray fox in southern Illinois. *J. Wildl. Manage.* 22:157-163.
- Litvaitis, J.A., J.A. Sherburne, and J.A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. *J. Wildl. Manage.* 50:110-117.
- Lockie, J.D. 1966. Territory in small carnivores. *Symp. Zool. Soc. Lond.* 18:143-165.
- Lord, R.D. Jr. 1961. A population study of the gray fox. *Am. Midl. Nat.* 66:87-109.
- MacDonald, D.W. 1980. Resource dispersion and the social organization of the red fox (Vulpes vulpes). Pages 918-949 in Chapman, J.A., and D. Pursley, eds. Worldwide furbearer conf. proc., Vol. II.
- , 1983. The ecology of carnivore social behavior. *Nature* 301:379-384.
- , F.G. Ball, and N.G. Hough. 1979. The evaluation of home range size and configuration using radio tracking data. Pages 405-424 in Amlaner, C.J., and D.W. MacDonald, eds. A handbook on biotelemetry and radio tracking. Pergamon press, Oxford.
- Mace, G.M., P.H. Harvey, and T.H. Clutton-Brock. 1983. Vertebrate home-range size and energetic requirements. Pages 32-53 in Swingland, I.R., and P.J. Greenwood eds. The ecology of animal movement. Clarendon Press, Oxford.
- McNab, B.K. 1963. Bioenergetics and the determination of home range size. *Am Nat.* 97:133-140.
- Messier, F., and C. Barrette. 1981. The social system of the coyote (Canis latrans) in a forested habitat. *Can. J. Zool.* 60: 1743-1753.
- Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* 37:223-249.

Mosby, H.S. 1971. Reconnaissance mapping and map use. Pages 119-134 in Giles, R.H., Jr., ed. Wildlife management techniques. The Wildlife Society by Edwards Brothers, Inc., Ann Arbor, Michigan.

Nicholson, W.S. 1982. An ecological study of the gray fox in east central Alabama. M.S. thesis, Univ. of Georgia. 106pp.

Nowak, R.M., and J.L. Paradiso. 1983. Walker's mammals of the world. Vol. I, 4th ed. The Johns Hopkins Univ. Press, Baltimore. 1362pp.

Richards, S.H., and R.L. Hine. 1953. Wisconsin fox populations. Wisconsin Conserv. Dept. Tech. Wildl. Bull. 6. 78pp.

Samuel, D.E., and B.B. Nelson. 1982. Foxes. Pages 475-490 in Chapman, J.A., and G.A. Feldhamer, eds. Wild mammals of North America. The John Hopkins University Press, Baltimore.
SAS Institute Inc. 1985.

SAS user's guide: statistics. Version 5 ed. Cary, N.C: SAS Institute Inc. 956pp.

Schoener, T.W. 1968. Sizes of feeding territories among birds. Ecology 49:123-142.

Seton, E.T. 1909. Life-histories of northern animals. An account of the mammals in Manitoba. Charles Scribner's Sons, N.Y. Vol. I, 667 pp. Vol. II, 1267pp.

Sheldon, W.G. 1949. Reproductive behavior of foxes in New York State. J. Mammal. 30:236-246.

----- 1950. Denning habits and home range of red foxes in New York State. J. Wildl. Manage. 14:33-42.

Smith, G.J., J.R. Cary, and O.J. Rongstad. 1981. Sampling strategies for radio-tracking coyotes. Wildl. Soc. Bull. 9:88-93.

Springer, J.T. 1979. Some sources of bias and sampling error in radio-triangulation. J. Wildl. Manage. 43:926-935.

----- 1982. Movement patterns of coyotes in south central Washington. J. Wildl. Manage. 46:191-200.

Sullivan, E.G. 1956. Gray fox reproduction, denning range, and weights in Alabama. J. Mammal. 37:346-351.

Sunquist, M.E. 1981. The social organization of tigers (Panthera tigris). Smithsonian Contrib. to Zool. No. 336. 98pp.

Trapp, G.R. 1978. Comparative behavioral ecology of the ringtail (Bassaricus astutus) and gray fox (Urocyon cinereoargenteus) in southwestern Utah. *Carnivore* 1:3-32.

Trapp, G.R., and D.L. Hallberg. 1975. Ecology of the gray fox. Pages 164-178 in Fox, M.W., ed. *The wild canids*. Van Nostrand Reinhold Co., N.Y.

van Orsdol, K.G., J.P. Hanby, and J. D. Bygott. 1985. Ecological correlates of lion social organization (Panthera leo). *J. Zool. Lond.* (A) 206:97-112.

von Schantz, T. 1981. Female cooperation, male competition, and dispersal in the red fox Vulpes vulpes. *Oikos* 37:63-68.

----- . 1984a. 'Non-breeders' in the red fox Vulpes vulpes: a case of resource surplus. *Oikos* 42:59-65.

----- . 1984b. Carnivore social behaviour- does it need patches? *Nature* 301:389-390.

Ward, R.M.P., and C.J. Krebs. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. *Can. J. Zool.* 63:2817-2823.

Wood, J.E. 1958. Age structure and productivity of a gray fox population. *J. Mammal.* 39:74-86.

Wood, J.E., D.E. Davis, and E.V. Komarek. 1958. The distribution of fox populations in relation to vegetation in southern Georgia. *Ecology* 39:160-162.

Wooding, J.B. 1984. Coyote food habits and the spatial relationship of coyotes and foxes in Mississippi and Alabama. M.S. thesis, Mississippi State Univ. 43pp.

Yearsley, E.F., and D.E. Samuel. 1980. Use of reclaimed surface mines by foxes in West Virginia. *J. Wildl. Manage.* 44:729-734.

PART IV

GRAY FOX ACTIVITY PATTERNS AND HABITAT USE

ABSTRACT

Gray fox (Urocyon cinereoargenteus) activity patterns and habitat use were determined from radio-telemetry data (Sept. 1986-Aug. 1987) on the Oak Ridge Reservation, east Tennessee. Foxes were generally active nocturnally (66.6% active), inactive diurnally (21.9% active), and less active during early morning (26.6% active) than evening (54.3% active). Chi-square tests comparing activity patterns based on seasons of food-type exploitation, relative food abundance, breeding cycle and degree of vegetative cover showed the most significant differences between months of high vegetative cover (foliage) (May-Oct.), when early morning and daylight activity levels were higher than in months of low (Nov.- Apr.) vegetative cover. A prey base study tentatively indicated that the winter small mammal population was most abundant in mature pine habitat, followed by oldfield, deciduous forest and young pine habitat, respectively; variation in trapping success between seasons and replicate grids, however, was high. Habitat utilization analysis showed that annually, foxes selected young pine more than expected relative to availability. Seasonal analysis based on food-type exploitation revealed that nocturnally, all habitat types were used in proportion to availability in winter and spring; in summer-fall young pine was used significantly more than expected. This may have been due

to high concentrations of blackberries (which ripen in summer) within this habitat type. A slightly higher selection of mature pine was observed in winter, and might be attributed to a higher concentration of small mammals (winter food source) within this habitat type. High daytime use of young pine habitat persisted year-round. Observed daytime resting sites were in thick early-successional vegetation, rocky ledges or underground holes. Suspected maternal dens were dug into the roots of windthrown trees. It appears that while territory sizes are relatively constant and adjusted to periods of food scarcity, shifts in habitat use may occur according to location of seasonally available foods.

INTRODUCTION

The wide geographic distribution of gray foxes (*Urocyon cinereoargenteus*) is a clue to their great behavioral plasticity in relation to habitat use and dietary flexibility. Currently, the gray fox ranges from extreme southern Canada through North and Central America to northern Venezuela and Columbia in South America, except for the Great Plains and parts of mountainous regions in the Northwest and Rockies in the U.S. and eastern Central America (Fritzell and Haroldson 1982). Current range therefore appears to be restricted by cool climates and boreal forests in the north, and by cool mountainous regions and unforested plains in the northern Great Plains (Fritzell and Haroldson 1982).

Studies of habitat utilization in several locales have confirmed the elastic behavior of gray foxes to their local surroundings, seasons and available habitat. In general the species is closely associated with brushy, wooded areas on rocky, rough terrain (Trapp and Hallberg 1975); in the eastern U.S., gray foxes are associated with deciduous forest (Hall 1981). In the Pacific states Grinnell et al. (1937) reported that gray foxes inhabit the Upper Sonoran and transition life zones, including chapparal-oak covered foothills below 2288 m.

Don and Rennolls (1985) suggested that habitat utilization is related to distribution of food, water and shelter. Trapp (1978) in Zion National Park, Utah, and Follmann (1973) in Illinois reported that gray foxes used old fields more than expected relative to availability within their home range, and use woodlands either proportionately to availability or preferentially over agricultural lands. Haroldson and Fritzell (1984), working in the Missouri Ozarks, found the converse to be true. Although frequency of use of each habitat type differed between foxes, the majority of individuals utilized mature oak-hickory woodlands most heavily, and oldfield habitat the least, during both the day and the night. The authors attributed habitat preference to the importance of dense vegetation as cover for gray foxes. Follmann (1973) and Yearsley and Samuel (1980) found that gray foxes used woodlands more during the day than night year-round, also suggesting the importance of woodlands as cover.

Fuller (1978) found that riparian habitat was used more heavily than expected by gray foxes in the central valley of California, and noted that riparian habitat was far superior to other habitats in its

abundance of important fox resources. Oldfield habitats and areas of human use were used more heavily than expected in the absence of available riparian habitat, and agricultural lands least. Hallberg and Trapp (1984), working in an area close to Fuller's study site, found that foxes spent 75.7% of the nocturnal period and 91.6% of daytime hours in the riparian zone along a stream, and the remainder of the time in agricultural areas. These authors suggested that heavier daytime use of woodlands was due to its cover value. Home range shapes coincident with the wooded riparian zone, as well as less selectivity of diurnal resting sites in spring, when vegetative cover was denser, lend support to this "availability of cover" hypothesis (Hallberg and Trapp 1984). Fuller (1978) did not relate habitat use to seasons.

Yearsley and Samuel (1980) found that although gray foxes in West Virginia generally used woodlands more than surface mines, and farmlands the least, proportional use changed seasonally. For example, 66% of nighttime locations were in woodlands in winter, but only 21% in October, when mines received the highest use. They attributed seasonal changes in habitat use to changes in the availabilities of preferred fox foods. Heavier use of reclaimed surface mines in spring and fall were attributed to the greater seasonal abundance of insects, berries and small mammals in these areas than in surrounding habitats. Insect and small mammal material appeared to be important in fox spring diet, while autumn olive (Eleagnus sp.) was the principal component identified in October fox scats. Small sample size, unavoidable error in radio-telemetry technique in an area of patchy habitats, along with an absence of statistical data analysis render conclusions in Yearsley

and Samuel's (1980) study only tentative. Lack of systematic dietary analysis or prey-availability assessment for relating to habitat use made much of their study conjecture rather than definitive fact. Haroldson and Fritzell (1984) found that large variation between habitat use patterns of individual foxes rendered significant differences between seasonal habitat utilization impossible to discern; they concluded that gray foxes are, overall, habitat generalists.

Wood et al. (1958) determined by scent lines and trapping that gray foxes in south Georgia used areas supporting mixed woods and cultivation over savannah pinelands, and used wooded areas with dense underbrush the least. The authors related these trends to declining abundance of important seasonal fox foods (especially rabbits, rodents, birds, insects, peanuts, persimmons, and plums) in the three vegetational types. It appears then, that gray foxes are habitat generalists, using available vegetation types opportunistically for food and cover.

An understanding of habitat use by gray foxes might provide insight into their wide geographic distribution, variation in home range sizes between geographic locations, study areas and/or individuals, and biological requirements of the species.

Knowledge of 24-hour and seasonal activity patterns is important in relation to temporal environmental and biological factors and their relevance to habitat use. Most studies indicate that gray foxes are generally nocturnal (Follmann 1973; Nicholson 1982; Grinnell et al. 1937; Trapp 1978; Yearsley and Samuel 1980; Haroldson and Fritzell 1984). Haroldson and Fritzell (1984) found that that foxes were active

at 53.7% of diurnal locations, activity typically decreased at sunrise, and increased sharply at sunset, continuing throughout the night.

Yearsley and Samuel (1980) reported that gray foxes were typically active at 24% of the daytime fixes. Nicholson (1982) reported that foxes were generally active from 1 hour before sunset to 1 hour after sunrise, and were generally inactive during the day, barring short movements within a chosen days resting area. Hallberg and Trapp (1984) also suggested that gray foxes made only local moves during daytime periods, and that peak activity occurred between 3 hour after sunset and 2 hours after sunrise.

More information is needed to clearly delineate habitat use in relation to active (foraging) and inactive (resting) periods as well as to seasonal availability of food and cover. This can be achieved only if an analysis of diet is conducted in conjunction with an assessment of food availability (by habitat and season), home range size, activity patterns and habitat use by gray foxes. In the current study, data on both annual diet (via scat analysis; see part II) and small mammal prey base were collected simultaneously with habitat-use and activity data on gray foxes. This presented a unique opportunity for testing the following null hypotheses: (1) seasonal shifts in diet did not influence habitat use in gray foxes (diurnally or nocturnally); and (2) seasonal availability of vegetative cover did not influence gray fox habitat use (diurnally or nocturnally).

STUDY AREA

The National Environmental Research Park (NERP), Department of Energy Oak Ridge Reservation (DOE, ORR), is located approximately 28 km west of Knoxville, Tennessee, and is operated by Martin Marietta Energy Systems. The NERP comprises approximately 50 km² of the Reservation's total 144 km². The study area was located within the NERP and lies between approximately 84° 16' to 84° 21' west longitude and 35° 56' to 35° 58' north latitude.

The NERP contains a diversity of vegetation community types. These include both natural and managed yellow pine forests, eastern red cedar barrens, oak-hickory forests, bottomland hardwood forests, and old fields, as well as several developed facilities for energy research and production. The Tennessee Valley Authority's Melton Hill Reservoir and Watts Bar lake which fringe the Reservation on the west, south and east, and numerous streams and springs throughout the area provide an abundance of wetland habitat and water for a variety of wildlife species. Several main and dirt roads dissect the Reservation, providing excellent vehicle access to most areas and tremendous advantage in gathering radio-telemetry data.

The geology of the Reservation is characteristic of the Southern Appalachian Ridge and Valley province. Parallel, southwest-northeast-oriented ridges separated by valleys (elevation ranging from 226 to 413 m above sea level) lend additional diversity to the landscape.

The DOE ORR has been protected from hunting and trapping since its purchase in 1942 until 1985, when managed hunts for white-tailed deer

(Odocoileous virginianus) were permitted. This protection in combination with the diversity of habitat types creates ideal conditions for an abundance and variety of animal species.

METHODS AND MATERIALS

Trapping

Foxes were captured in No. 1.5 Victor soft-catch leg-hold traps using dirt-hole sets and drags. Attractants included fox urine, fox gland lures, pork cracklings, fish oil and muskrat oil. Traps were concentrated on the ORR NERP along dirt roads and powerlines. The first several foxes trapped were anesthetized with 5-10 mg/kg ketamine hydrochloride (Ketaset). After it became apparent that gray foxes become submissive when grasped by the back of the neck, foxes were handled without drugs using methods adapted from Nicholson (1982). Each animal was fitted with a radio-collar equipped with a mercury tip-switch activity sensor (Telonics) in the 150.3-151.84 MHz band. Ear tags also were attached for on-sight identification.

Sex, age (juvenile or adult) and overall physical condition were noted. Body measurements taken included weight, front and hind pad length, pes, tail length, total length, girth, neck circumference and ear length. Animals were released at the trap site.

Radio Telemetry

Receiving stations (n=138) were established on the NERP based on proximity to radio-collared gray foxes, angle between stations, topography, ease of location on study-area maps, and distance from electromagnetic interference (except where unavoidable for obtaining adequate angles). Animals were located with a 4-element hand-held Yagi antenna and a Telonics portable receiver by triangulation using the "loudest signal method" (Springer 1979). An azimuth was obtained on one or more foxes from a station using a Suunto KB-14 hand-bearing magnetic compass, the vehicle quickly driven to a second station and another azimuth taken. Often 3 or more azimuths were obtained to achieve an angle as close to the 90° optimum (Heezen and Tester 1967) as possible, hence increase accuracy. Angles less than 45° and greater than 135° were discarded. Locations where poor signals, signal bounce or too great a time lapse between bearings (> 5 minutes, or less if the animal seemed to be moving rapidly) interfered were discarded. Fox identification number, date, time, compass bearings, stations, quality of signal (if accuracy was in doubt) and activity were recorded. Initially (September-November 1986), each animal was located at 1-hour intervals one night each week between 1600-0800 hrs. When it was realized that all radio-collared foxes could be monitored on the same night with little sacrifice of information gathered (Smith et al. 1981; Dunn 1977) if locations were taken every 2 hours instead, this sampling regime was adopted (December 1986-August 1987). All field azimuths were converted into UTM X,Y coordinates by computer program "Convxpoly"

(Boyle 1986). All locations were hand-plotted onto a 1:24000 scale UTM grid by month for each fox; daytime and nighttime locations were separated for diurnal and nocturnal habitat analysis.

Data Analysis: Activity

For detection of daily activity cycles, the 24-hour day was partitioned into 4 time periods. Morning crepuscular hours were defined to include 0-.50 hours prior to sunrise and approximately 1.5-2.0 hours subsequently (for a total of 2 hours); evening crepuscular hours included 1.5-2.0 hours prior to sunset and 0-.50 hours preceding (for a total of 2 hours); nighttime included the hours between "sunset" and "sunrise" categories (darkness), and daytime included the hours between "sunrise" and "sunset" categories. "Activity" was defined as any motion that might tip the activity-sensing mercury tip-switch within the radio-transmitter. The percent of "active" locations within each time period was calculated both annually and seasonally.

Chi-square goodness of fit tests (Steel and Torrie 1980) were performed to detect differences in activity levels within the 24-hour cycle between seasons. Data were pooled for all animals (n=12), thus masking individual differences in activity patterns. Four sets of seasons were tested. First, three seasons based on food-category exploitation included "animal prey" (January-April), "insect prey" (May) and "fruit prey" (June-December) (part II) were tested. A second set of 2 seasons based on relative abundance of foods ("scarce" included "animal prey"; "abundant" included "insect prey" and "fruit

prey" as described above) were tested to eliminate any bias resulting from small May sample size (part II). A third set of 3 seasons were based on breeding cycle dates, including "breeding" (January-March); "pup-rearing" (April-July), and "prebreeding" (August-December) as reported for foxes in the southeast (Layne 1958; Wood 1958; Nowak and Paradiso 1983; Sullivan 1956). The fourth set of 2 seasons were based on a subjective determination of degree of vegetative cover (seasonal foliage). "High" vegetative cover included May-October; "low" cover included November-April.

Small Mammal Sampling

The relative abundance of small mammals among 4 habitat types was assessed by live-trapping in 4 seasons: autumn (October, 1986), winter (January and February, 1987), spring (April and May, 1987), and summer (June and July, 1987). There were 2 grids in each of the 4 habitat types as defined above. Specifically, plots were located in deciduous forest; mature, (> 30 years) periodically burned, managed monocultures of loblolly (*Pinus taeda*) pine stands; young (≤ 15 years), unburned, managed monocultures of loblolly pine stands with a dense understory; and oldfield (powerline right-of-ways) habitat. All grids were located within areas of known use by radio-collared study animals. Small mammal populations were sampled with Sherman live traps spaced at 10 m intervals in a 70 X 70 m grid (64 traps per grid). Similar methods have been used in other small mammal studies on the ORR (Deuser et al. 1976; Smith 1976; Johnson et al. 1979; Kitchings and Levy 1981; Seagle

et al. 1984). For autumn trapping a 4-day acclimation period was permitted, while traps remained open and unset, followed by 3 consecutive days of trapping for a total of 384 trapnights per habitat. For winter, spring and summer trapping, this regime was reversed, with a 3-day acclimation period followed by 4 consecutive days of trapping for a total of 512 trapnights per habitat type per season, or 1920 trapnights per habitat type annually. Peanut-butter and oats were used for bait. Small mammals were individually marked using colored acrylic paints, and released at the trap site after species, individual marking and trap location were noted. Differences in overall small mammal population sizes between habitat types and seasons were tested by ANOVA (SAS Inst. Inc. 1985).

Data Analysis: Habitat Utilization

A vegetation map (1:24000 scale) delineating 4 coarsely defined habitat types was created from a larger scale, more detailed forestry map of the ORR. Habitat types included deciduous forests; mature (> 15 years) yellow pines; young, (≤ 15 years) yellow pine monocultures, and oldfield habitat. The "deciduous forest" classification included primarily mature mixed hardwoods and mixed pine-hardwood stands. The few mature, managed hardwood monocultures contained within the study area also were classified with the deciduous woods habitat type. The "mature pine" habitat classification included natural pine stands, cedar stands (Juniperus virginiana) and managed monocultures of shortleaf pine (Pinus echinata) and loblolly pine > 15 years old.

Relatively clean understories were maintained by periodic burning of mature, managed pine stands. The "young pine" habitat classification included planted monocultures of yellow pine ≤ 15 years old. These stands were not burned, and contained a dense, brambly understory of Japanese honeysuckle (Lonicera japonica), blackberry (Rubus sp.), sumac (Rhus sp.) and greenbriar (Smilax sp.). "Oldfield" habitat included primarily early successional habitat, such as telephone and powerline right-of-ways. Vegetation in these areas included broomsedge (Andropogon virginicus) and other grasses, Japanese honeysuckle, blackberry, greenbriar, sumac, and a few young pine and hardwood seedlings. Dirt and paved roads and roadsides, areas of human use such as buildings, and beetle-kill or recently cut-over areas (≤ 15 years) were also included in this coarse habitat classification. Averaged among composite home ranges for 12 gray foxes, deciduous forest comprised approximately 47%, mature pine 19%, young pine 3%, and oldfield 31% of the landscape within the study area.

Plots of fox locations were superimposed onto the vegetation map on a light table, and the number of fixes counted in each vegetation type using methods adapted from Trapp (1978). All locations were used in habitat analysis, including predominantly locations within an animal's home range, and a few which were subjectively omitted as "excursions" in home range calculations. The proportion of available habitat within an animal's home range was determined by superimposing the composite home range map onto the vegetation map, and using a dot grid acetate overlay to count acreage of the 4 types within that area (Mosby 1971). Acreage was converted to km^2 .

Habitat choice by individual foxes was evaluated using a habitat-affinity index (Cairns and Telfer 1980) to eliminate bias from differential habitat availability within home ranges. The index was calculated by dividing the proportion of a given habitat type within an individual's home range into the proportion of locations in that habitat type. Index values of 1.0 indicate use of the habitat type in proportion to its availability. Values greater than 1.0 show selection of that habitat, while values less than 1.0 indicate avoidance relative to its availability.

Chi-square goodness of fit tests (Steel and Torrie 1980) were applied to total location frequencies to test the null hypothesis that foxes used each habitat type in proportion to its occurrence within the study area, on an annual and seasonal basis. Data were pooled for all animals ($n=12$), thus individual differences in habitat use were masked. The mean proportion of 4 habitat types within the home ranges of all study animals was utilized to derive "expected" Chi-square values for habitat utilization to eliminate bias in differential habitat availability. Chi-square tests also were used to examine seasonal changes in habitat utilization. Several sets of "seasons" were tested, as defined previously (breeding cycle; food availability; food-type exploitation and degree of vegetative cover). Diurnal and nocturnal habitat use were treated separately for all statistical tests to detect any existing differences in habitat utilization during these periods.

RESULTS AND DISCUSSION

Trapping

A total of 937 trapnights yielded 17 captures of 16 gray foxes. Of these, one escaped upon approach, and 2 were not collared due to trap-related injuries. Radio-collared foxes included 6 males and 7 females. Physical data on captured animals are summarized in Appendix, Table A-3.

Activity

Activity was recorded for 2106 locations. Gray foxes were generally active nocturnally (66.6% activity recorded; $n=1354$), inactive diurnally (21.9% activity recorded; $n=393$) and less active during morning crepuscular hours (26.6% activity recorded; $n=94$) than evening hours (54.3% activity recorded; $n=265$) (Figure IV-1). This pattern appeared to remain fairly consistent year-round, however Chi-square goodness of fit tests comparing seasons based on high and low vegetative cover, breeding cycle, food-type exploitation and relative seasonal abundance of food revealed some significant differences between seasonal activity levels, specifically in the early morning and daylight hours. There were significant differences ($\chi^2=22.305$, $df=6$, $p<0.005$) between 3 activity levels during seasons of food-type exploitation, with a lower level of sunrise activity in winter (January-April: animal prey) relative to spring (May: insect season) or summer-fall (June-December),

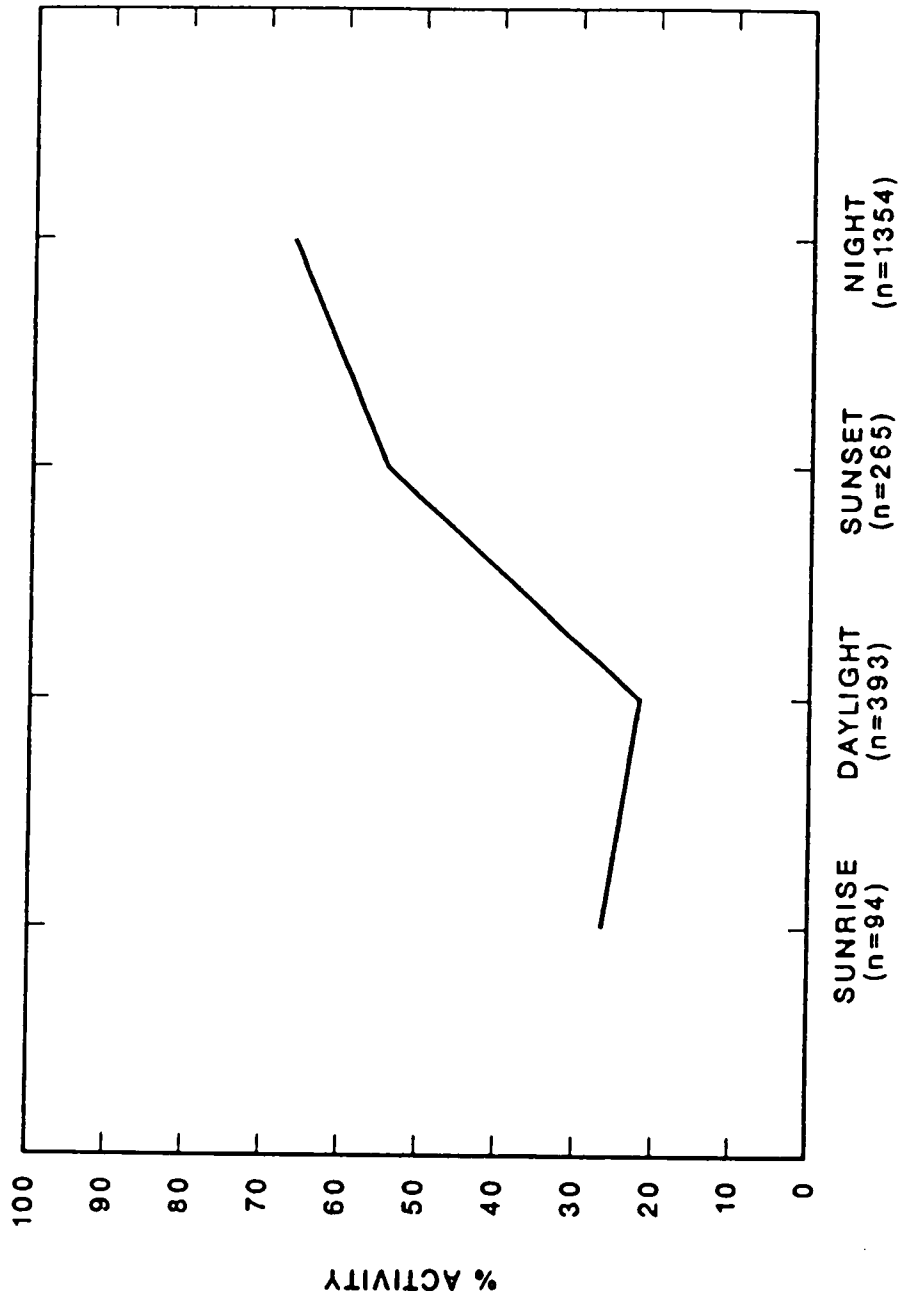


Figure IV-1. Annual percent activity recorded for radio-telemetry locations during sunrise, daylight, sunset, and night time periods for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

and a higher level of sunrise activity in spring relative to other seasons (Table IV-1). To eliminate potential bias posed by a smaller spring (May) sample size, a Chi-square test was conducted pooling May with summer-fall (fruit) seasons for generalized "scarce" and "abundant" food seasons. The same trend was detected with this grouping. There was a significant difference between seasons ($\chi^2=17.853$, $df=3$, $p<0.0005$), with lower levels of activity at sunrise during "scarce" season relative to abundant, and higher sunrise activity levels in abundant season relative to scarce season (Table IV-1).

A significant difference in activity patterns among the 3 breeding seasons was detected ($\chi^2=29.791$, $df=6$, $p<0.0005$). Lower sunrise and daylight activity levels were observed during breeding season (January-March) relative to pup-rearing or prebreeding seasons, and higher daylight activity levels in pup-rearing season relative to breeding or prebreeding seasons (Table IV-1).

A significant difference ($\chi^2=32.277$, $df=3$, $p<0.0005$) in activity patterns was detected between months of low vegetative cover (November-April) and high vegetative cover (May-October). Lower sunrise and daylight activity levels occurred during months of low vegetative cover relative to high, and relatively higher activity occurred during these hours in months of high vegetative cover (Figure IV-2; Table IV-1).

Significant differences between 24-hour activity levels among seasons may have been an artifact of numerous subsets of the same months. It is difficult to distinguish which environmental or

Table IV-1. Activity patterns, on an annual and seasonal basis, for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

Time Period	% Active Locations			
	Sunrise	Daylight	Sunset	Night
Annual (n=2106)	27	22	54	67
Breeding (n=655) (January-March)	0	12	48	61
Pup-rearing (n=682) (April-July)	35	32	67	68
Prebreeding (n=769) (August-December)	27	19	49	70
Animal food (n=884) (January-April)	5	19	57	59
Insect food (n=148) (May)	67	22	75	80
Plant food (n=1074) (June-December)	28	24	50	72
Abundant food (n=1222) (May-December)	32	24	52	73
Scarce food (n=884) (January-April)	5	19	57	59
High vegetative cover (n=962) (May-October)	36	27	56	73
Low vegetative cover (n=1144) (November-April)	7	16	53	62

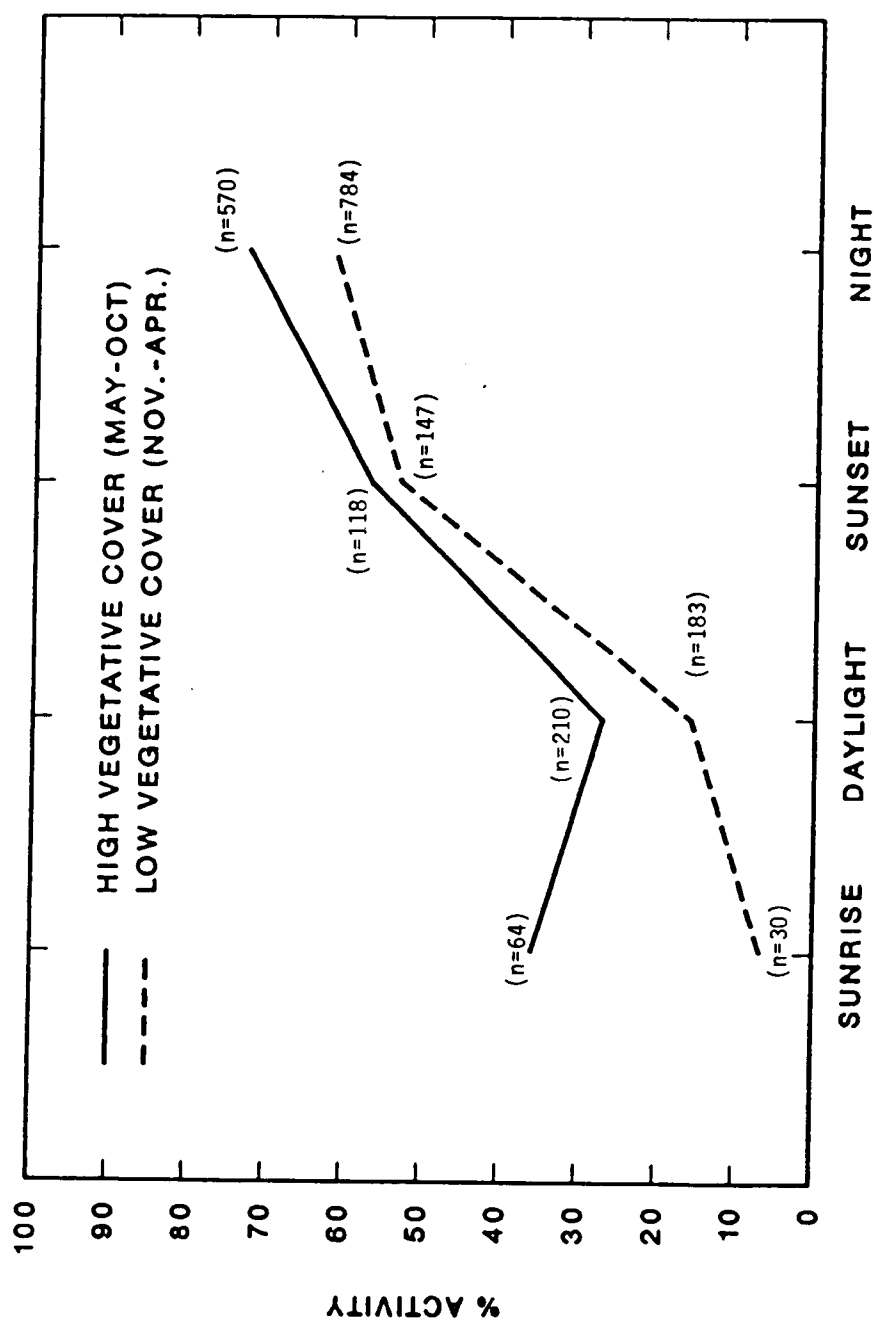


Figure IV-2. Percent activity recorded for radio-telemetry locations during seasons of high (May-Oct.) and low (Nov.-Apr.) vegetative cover during sunrise, daylight, sunset, and night time periods for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

biological circumstances, if any, contributed to these differences. It is of interest to note, however, that all significant differences among seasons compared occurred between winter and spring-summer-fall months. The grouping of months based on level of vegetative cover yielded the highest (most significant) Chi-square value, suggesting that this factor may exert a greater influence on early morning and daylight activity levels than breeding cycle, food-types exploited or relative seasonal abundance of food. The relatively higher concealment value offered by heavy vegetative cover may have contributed to the higher activity levels observed during early morning and daylight hours when the risk of visibility was greater. Hallberg and Trapp (1984) also noted substantial differences in diurnal activity levels between spring (low activity levels; sparse vegetative cover) and summer (higher activity levels; greater vegetative cover), and attributed this to seasonal differences in vegetative cover. Nocturnal activity levels were not as distinct between seasons, possibly since darkness reduced the influence of cover.

Undoubtedly, other biological and/or environmental factors contributed to these differences as well. Colder winter temperatures or lower energy levels of foxes due to lower prey availability may contribute to lower winter sunrise and daytime activity levels, although the opposite may also be argued. Sunquist (1981), for example, reported lower diurnal activity levels during "hot" season for tigers, and attributed this to heat avoidance. Perhaps higher levels of daylight activity observed during "pup-rearing" season (April-July) were due to greater energy demands on parent (especially female) foxes,

as well as the added demand for food by young offspring. Sunquist (1981) suggested that a close correlation between activity levels for predators and prey exists. While probably unnecessary during frugivorous or insectivorous seasons, closely coinciding activity periods may have become important for foxes in winter when only animal foods were available. More "flexible" activity schedules during spring, summer and fall months may have been replaced by the greater necessity for nocturnal activity during winter months. In conjunction with this, perhaps an "unlimited" food supply during spring, summer and fall months provided surplus energy, allowing for "luxury" energy expenditure for daylight exploration, foraging and other movement.

Relative Abundance of Small Mammals

Small mammal trapping success across 4 seasons averaged 3.9/100 trap nights in deciduous forest habitat; 3.6/100 trap nights in mature pine habitat, and 2.6/100 trap nights in oldfield and in young pine habitat (Appendix, Table A-7). Nine species of small mammals were captured (Appendix; Table A-8), including cricetid rodents, the white-footed mouse (Peromyscus sp.), golden mouse (Ochrotomys nuttalli), eastern harvest mouse (Reithrodontomys humulis) and cotton rat (Sigmodon hispidus); a murid rodent, the house mouse (Mus musculus); sciurid rodents, the chipmunk (Tamias striatus) and the southern flying squirrel (Glaucomys volans), and 2 insectivores, the shorttail shrew (Blarina brevicauda) and least shrew (Cryptotis parva). It is of interest that no pine voles (Microtus pinetorum) were trapped during

the entire year, although they were the most commonly occurring small mammal item in winter gray fox diet (part II), and were reported as a commonly occurring species in several previous studies conducted using similar methods on the ORR (e.g. Dunaway and Kaye 1961; Johnson et al. 1979; Seagle et al. 1984). It is also of interest that only 4 cotton rats were trapped, and then only during the summer trapping period. They were reported in an earlier study conducted at ORR (Dunaway and Kaye 1961) as a commonly occurring species between 1957 and winter 1959-60, when a severe winter virtually exterminated their populations. In more recent studies this species is only rarely noted (e.g. Johnson 1979; Seagle et al. 1984).

Of the total number of small mammals trapped ($n=244$), 30.7% were trapped in deciduous forest habitat; 28.7% in mature pine habitat, and 20.3% in young pine and in oldfield habitat (Appendix, Table A-7). Variation among seasons and replicate grids within habitat types was high. ANOVA detected no significant differences in the relative population size of small mammals among habitat types ($p=0.4639$). Differences among seasons were significant at the $\alpha=0.05$ level ($p=0.0168$); Tukey's studentized range test detected significant differences between autumn (mean number of individuals captured is 3.125) and spring (mean=10.875) overall small mammal population levels.

Since small mammal prey was utilized most heavily by gray foxes in winter (part II), only differences in relative the population size of small mammal prey between habitat types in winter trapping was examined. ANOVA detected no significant differences in relative abundance among habitat types ($p=0.2811$), probably due to high variance

among replicate grids. Nonetheless, Appendix, Table A-7 indicates that in winter (1986-1987) alone, the small mammal population in mature pine habitats was at least equally as high as in other habitat types (grid 1), and possibly much higher (grid 7). Pooled data from replicate grids indicate that, of total winter captures, 44.8% were habitat; 25.4% in oldfield habitat; 19.4% in deciduous forest, and only 10.4% in young pine habitat (Figure IV-3).

A comparison of other studies conducted on the ORR within identical habitat types indicate that size of small mammal populations either fluctuate between and within habitat types from year to year, or sampling techniques are not adequate for proper population assessments. The discrepancy between lack of capture and high winter consumption of pine voles by foxes further indicates some bias in sampling technique. Deuser et al.'s (1976) 1972-1974 trapping data indicated that, of deciduous and pine (age unknown; probably young) habitats, deciduous woods contained a greater abundance of small mammals. In winter, 58% of small mammal captures were in deciduous woods, and 41% in pine habitat. Johnson et al. (1979) reported that in 1975, mature pine habitat contained the greatest relative abundance of small mammals, followed by oldfield and deciduous forest habitat, respectively. Smith (1976) also reported a much higher 1975 small mammal standing crop biomass in ORR mature loblolly pine plantations than in mixed hardwood habitat. Trapping conducted in 1979-1980 (Seagle et al. 1984) indicated that oldfield habitat contained a greater abundance of small mammals than pine plantation (age not specified; probably mature) and deciduous

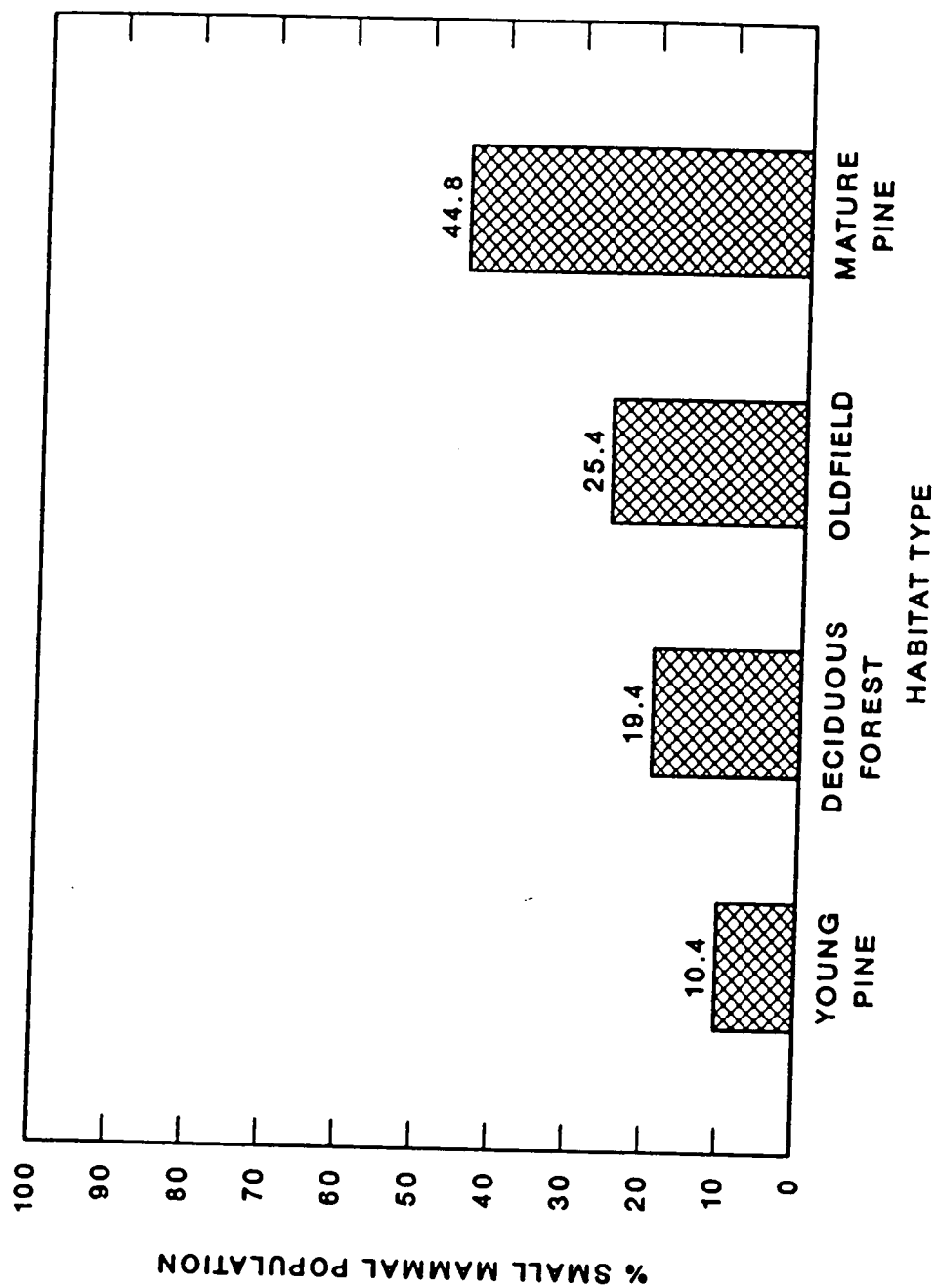


Figure IV-3. Relative abundance of small mammal populations in 4 habitat types in winter 1986-1987, on the Oak Ridge Reservation, east Tennessee.

forest, respectively. Seagle et al. (1984) noted a small mammal population collapse in pine habitat in 1981, and those data were omitted from their analyses. As noted previously, Dunaway and Kaye (1961) reported a cotton rat population crash during the severe 1959-1960 winter. Thus, small mammal population fluctuation appears to be common, and must be considered on a year to year, or even a season to season basis.

In 3 of the 4 ORR studies reviewed, it appeared that mature pine and oldfield habitats contained a greater abundance of small mammals than deciduous woods. Although pooled data from all seasons in the current study indicated a high small mammal population in deciduous woods and mature pine habitats relative to young pine and oldfield habitat types, pooled data from winter only from the current study indicated, in accordance with Smith (1976), Johnson et al. (1979) and Seagle et al. (1984), that the small mammal population ranked highest in mature pine stands, followed by oldfield, deciduous forest and young pine habitat, respectively. If seasonal diet affects gray fox habitat use, a winter shift towards higher utilization of mature pine and/or oldfield habitat (relative to its proportional availability) by might be hypothesized.

Habitat Utilization

A total of 2247 radio locations were recorded between September 1986 and August 1987 to estimate habitat utilization by 12 gray foxes. Of the total sample, 1577 radio locations were obtained between sunset

and sunrise, and 670 between sunrise and sunset. Most locations were determined nocturnally and crepuscularly, since most gray fox activity occurs during these hours (Trapp 1978; Trapp and Hallberg 1975; Yearsley and Samuel 1980; Fritzell and Haroldson 1982; the current study). The predominantly nocturnal activity of gray foxes in the current study was used to infer that most daytime radio locations represented habitats used for resting, while most nighttime locations represented habitats used for foraging and travel. Duration of radio-tracking, monthly number of radio-locations, and the eventual fates of the 13 collared foxes are presented in Appendix, Figure A-1.

Affinity index values for annual nocturnal and diurnal habitat utilization for individual foxes are shown in Tables IV-2 and IV-3, respectively. In agreement with Haroldson and Fritzell (1984), variation among individuals was great, and patterns of habitat utilization difficult to discern.

On an annual basis, nocturnally gray foxes preferred young pine, used deciduous forest and oldfield habitat in proportion to their availability, and used mature pine less than expected ($\chi^2=50.041$, $df=3$, $p<0.0005$) (Table IV-4). Diurnally, young pine habitat was utilized in far greater proportion than its availability, with oldfield, mature pine, and deciduous forest habitat used approximately in proportion to their availability ($\chi^2=188.257$, $df=3$, $p<0.0005$). There was a significant difference between diurnal and nocturnal habitat use ($\chi^2=35.995$, $df=3$, $p<0.0005$), with foxes selecting for young pines during daylight over nighttime hours. Mature pine, oldfield and deciduous forest habitat were used approximately in proportion to their

Table IV-2. Diurnal habitat affinity index values for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987. Index values of 1.0 indicate use of that habitat in proportion to its availability; greater than 1.0 indicates higher use, and less than 1.0 indicates lower use than expected if animals utilized habitat types randomly.

Habitat Type	Fox ID											
	58	69	76	82	84	62	63	64	66	74	78	80
Young pine	11.00	2.00	---	0.50	0.31	0.83	0.00	12.33	4.86	---	3.00	0.00
Deciduous forest	0.39	1.26	1.27	0.01	0.94	0.86	0.77	0.58	0.91	1.24	1.12	0.89
Oldfield	0.00	0.73	0.74	0.89	1.00	1.05	1.55	1.04	0.68	1.00	0.56	0.00
Mature pine	2.94	0.42	0.01	1.46	0.46	1.22	0.84	0.23	0.17	0.50	1.57	3.13

Table IV-3. Nocturnal habitat affinity index values for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987. Index values of 1.0 indicate use of that habitat in proportion to its availability; greater than 1.0 indicates higher use, and less than 1.0 indicates lower use than expected if animals utilized habitat types randomly.

Habitat Type	Fox ID											
	58	69	76	82	84	62	63	64	66	74	78	80
Young pine	0.00	1.20	---	1.00	3.00	0.50	0.66	4.00	1.28	---	1.50	0.00
Deciduous forest	0.84	1.00	1.16	0.82	0.63	0.59	1.00	0.93	1.15	1.16	0.84	0.68
Oldfield	1.03	1.03	1.17	1.19	1.44	1.62	1.32	1.04	1.05	0.96	0.89	2.30
Mature pine	1.53	0.83	1.00	1.00	1.08	0.67	0.53	0.54	0.39	0.71	1.64	0.00

Table IV-4. Diurnal and nocturnal habitat utilization, on an annual and seasonal basis, for 12 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

Time Period	% Habitat			
	Young Pine	Deciduous Forest	Old Field	Mature Pine
Total available habitat	3	47	31	19
Total diurnal locations (n=670)	12	47	25	16
Winter (n=202) (January-April)	9	46	27	18
Spring (n=49) (May)	4	53	33	10
Summer-Fall (n=419) (June-December)	14	45	24	16
Abundant (n=468) (May-December)	13	47	25	15
Scarce (n=202) (January-April)	9	46	27	18
Low vegetative cover (n=310) (November-April)	12	46	25	17
High vegetative cover (n=360) (May-October)	12	47	26	15
Total nocturnal locations (n=1577)	6	46	33	15
Winter (n=713) (January-April)	4	48	30	18
Spring (n=100) (May)	0	49	30	18
Summer-Fall (n=764) (June-December)	7	45	36	12
Abundant (n=864) (May-December)	7	45	36	12

Table IV-4 (continued).

Time Period	% Habitat			
	Young Pine	Deciduous Forest	Old Field	Mature Pine
Scarce (n=713) (January-April)	4	48	30	18
Low vegetative cover (n=1054) (November-April)	7	47	29	17
High vegetative cover (n=523) (May-October)	3	45	39	13

availability, both during the daytime and nocturnally (Table IV-4). Young pine habitat provided an excellent source of dense, brambly, protective cover for a potential daytime resting place.

It is more informative to examine habitat use according to seasonal activities of gray foxes such as food-type exploitation (part II), the annual breeding cycle, and according to environmental factors such as the potential concealment value and insulation value afforded by vegetative cover.

Chi-square tests for each of the three seasons defined by food-types exploited (part II) revealed that nocturnally, habitat types were not utilized significantly disproportionately to availability in winter ($\chi^2=2.48$, $df=3$) or spring ($\chi^2=6.652$, $df=3$). During the the summer-fall season, however, young pine habitat was utilized in greater proportion to its availability, while mature pine was used in smaller proportion to its availability; deciduous forest and oldfield habitat were used approximately in proportion to their availability ($\chi^2=53.692$, $df=3$, $p<0.0005$) (Table IV-4).

There were significant differences in habitat use among food-type exploitation seasons ($\chi^2=30.187$, $df=6$, $p<0.0005$), with use of young pine increased from less than expected in winter and spring to more than expected in summer-fall. Deciduous forest habitat appeared to be utilized approximately in proportion to its availability year-round. Oldfield habitat was used slightly less than expected in winter, as expected in spring, and slightly more than expected in summer-fall. Mature pine habitat did not appear to be avoided as heavily in winter months as in other months (Table IV-4).

Habitat use was significantly different between "abundant" and "scarce" food seasons ($\chi^2=20.384$, $df=3$, $p<0.0005$). During spring-summer-fall seasons combined ("abundant" food season), young pine habitat was utilized more than expected, deciduous and oldfield habitat were utilized in proportion to availability, and mature pine was avoided relative to its availability by gray foxes (Table IV-4).

The observed seasonal switch in nocturnal (foraging) habitat utilization might be due to seasonal flux in the location of available foods. During winter, when animal prey was utilized most heavily by gray foxes, it appeared that no single habitat type was preferred by gray foxes, although compared to spring and summer-fall a slight selection toward mature pine habitat utilization was observed (Table IV-4). Since the prey base survey suggested that small mammals, including Peromyscus and other species known to be fox foods (e.g. part II; Scott 1955; Yoho and Henry 1972), were more abundant in the mature pine habitat in winter, a heavier use of this habitat by gray foxes for prey exploitation might be expected if indeed food availability influenced habitat use by foxes. Other important winter foods, such as rabbits and white-tailed deer (carrion, probably), may have influenced fox habitat utilization differently, if at all. During spring, when 17-year locusts were a heavily exploited food source (part II), no habitat preference was observed (Table IV-4). Perhaps this food source was so abundant that little search effort was necessary; alternatively, perhaps the locusts appeared equally in all habitat types defined. During summer and fall, young pine habitat contained an abundance of seasonally available blackberries and other foods. Oldfields also

contained an abundance of blackberries (but were used only slightly more than expected). Deciduous woods contained squaw root (Conopholis americana), cherries (Prunus sp.) and persimmons (Diospyros virginiana), all heavily-used food items by gray foxes during the June-December months (part II). Deciduous forest was used more than other habitats (although not more than expected relative to its availability) simply because it comprised a large proportion (47%) of total habitat types. Mature pines represented a habitat containing a paucity of foods used by gray foxes during the spring, summer and autumn months. This may have been a contributing factor to the avoidance of this type relative to its availability by gray foxes during this time period (Table IV-4).

Chi-square tests for diurnal habitat use within each of 3 "food-type exploitation" seasons revealed that foxes utilized young pine significantly more than expected in the winter ($X^2=24.869$, $df=3$, $p<0.0005$) and summer-fall ($X^2=178.966$, $df=3$, $p<0.0005$) seasons, and all other habitat types in proportion to their availability. In springtime foxes used all habitats approximately according to their availability ($X^2=2.612$, $df=3$). A comparison of diurnal habitat use between these seasons revealed no significant difference ($X^2=9.457$, $df=6$), however (see Table IV-4).

In both "abundant" ($X^2=173.286$, $df=3$) and "scarce" ($X^2=24.869$, $df=3$) food seasons, diurnal use of young pines was significantly higher than expected, and all other habitat types were used proportionately to availability (Table IV-4). A comparison of these 2 seasons revealed no significant difference ($X^2=2.401$, $df=3$) in habitat use (Table IV-4).

No significant difference ($\chi^2=0.684$, $df=3$) was detected in diurnal habitat utilization between seasons of high or low vegetative cover (Table IV-4). During seasons of both high ($\chi^2=95.945$, $df=3$, $p<0.0005$) and low ($\chi^2=93.05$, $df=3$, $p<0.0005$) vegetative cover, young pine was selected significantly more than expected; other habitat types were used in proportion to their availability (Table IV-4).

It appears then, that diurnal habitat selection was not influenced by seasonal availability of foods, but instead by the year-round cover value of dense, brambly, protective young pine habitat. Nicholson (1982) also noted no change between diurnal resting sites between summer and winter. Other studies (e.g. Nicholson 1982; Wooding 1984) also suggest that blackberry thickets, honeysuckle tangles, dense thickets of hardwood sprouts and other areas of dense vegetation are common diurnal resting sites used by gray foxes. Although this habitat type was not likely to provide for all foraging needs, it apparently did provide excellent daytime concealment and protection for gray foxes year-round.

Inherent error involved in radio-telemetry techniques in an area of small, patchy habitats, in conjunction with high variation among individual habitat preferences render the above conclusions merely tentative. Such variation in fact, suggests, in agreement with Haroldson and Fritzell (1984) that gray foxes are indeed, habitat generalists. This might account for contradictory accounts of gray fox habitat preference among studies, as well as add insight into the wide geographic distribution of the species.

Daytime Resting Sites and Dens

Daytime resting sites and dens were verified by walk-ins on 15 occasions (Appendix, Table A-9). On 4 occasions foxes were resting in a powerline or telephone line right-of-way in dense thickets of early-successional vegetation such as blackberry, greenbriar, honeysuckle tangles and sumac, often within a gully. Foxes 62, 64 (female) and 69 (male) were frequently located by radio-telemetry simultaneously in the same vicinity along the same powerline; 62 and 64 were located (by walk-ins) in the same resting site on different occasions. On one occasion female 78 was discovered near some office buildings, well beyond her usual home range boundaries. Female 74 and male 76, probably a mated pair, were found together in a recently cut-over lot near a paved road, beneath dense brush, (possibly inside of a hole). All of these sites were considered "oldfield" in the habitat-classifications of the current study.

On two occasions foxes were in young pine habitat, under extremely dense, brambly vegetation. Nicholson (1982) also reported areas of dense vegetation as common daytime resting sites for foxes in Alabama.

On 7 occasions resting sites (including dens) were located in deciduous woods. Female 78 appeared to frequently use (verified twice, but located by radio-telemetry often) a "cave" den located in a rocky area at the edge of deciduous forest, immediately adjacent to a telephone line right-of-way. A third time she was in a young pine-hardwood forest with a great deal of slash on the forest floor. Female 66 was located in a similar habitat type within her home range. Male

82 was located in a hole "tunnelled" into a natural drainage gully near a small stream, also within a hardwood forest. Two dens (belonging to females 66 and 74, respectively) were located in May, and suspected of being maternal dens. Both were tunnelled into the upturned roots of windthrown trees, within a deciduous forest habitat. Male fox 65, not monitored for a sufficient length of time to warrant discussion, was located dead, probably from trap-related injuries, in a den located in an abandoned woodchuck hole in a deciduous woods; it was not known whether he used this den as a diurnal resting site. Other studies (e.g. Grinnell et al. 1937; Sullivan 1956; Trapp and Hallberg 1975; Follmann 1973; Nicholson 1982) also noted maternal den sites under the roots of windthrown hardwood trees, in underground burrows dug by woodchucks or foxes, as well as in brushpiles, tree cavities, hollow logs and other well-hidden locations. No daytime resting sites were ground-truthed in mature pine habitat.

Protection from visibility appeared to be the single common denominator between diurnal resting sites selected by gray foxes. Thick, brambly vegetative cover, most commonly found in early-successional oldfield or young pine habitat appeared to serve this function as well as underground retreats or dens within the roots of windfallen trees, most commonly noted in deciduous woods. Several other studies have revealed the diversity of gray fox den and resting sites, including under rocky outcrops, hollow logs, tree cavities, brush piles, slab piles, abandoned woodchuck dens, areas of dense vegetation, or other well-concealed locations (Richards and Hine 1953;

Grinnell et al. 1937; Nicholson 1982; Wooding 1984; Hallberg and Trapp 1984).

This small "subsample" of (verified) diurnal resting sites indicated that young pine habitat was indeed utilized diurnally in greater proportion than its availability. In contrast to results of Chi-square tests based on radio-telemetry data however, ground-truthing suggested that oldfield habitat was used diurnally somewhat more than expected. Possibly a low walk-in sample size was inadequate for "subsampling" the accuracy of radio-telemetry data. Alternatively, error inherent in radio-telemetry techniques, compounded by the elongated, narrow shape of most powerline right-of ways may have occasionally misplaced oldfield locations, potentially leading to an underestimation of oldfield habitat utilization.

SUMMARY AND CONCLUSIONS

The importance of concealment in influencing gray fox activity patterns was suggested by relatively higher activity levels at night, when darkness afforded some protection from visibility. This factor was further emphasized by the apparent influence of vegetative cover on activity patterns and diurnal habitat use. Significantly higher sunrise and daylight activity levels were observed between May and October, when thick vegetative growth afforded excellent cover, than between November and April when most leafy vegetation was absent. Significantly higher year-round diurnal (but not nocturnal) use of

young pine habitat relative to its availability also suggested the importance of dense vegetation for its concealment value to gray foxes.

Differences in habitat utilization between diurnal, predominantly inactive, and nocturnal foraging periods, as well seasonal changes in nocturnal habitat use not observed in the day suggested that factors other than cover entered into nocturnal habitat selection. While nocturnally, habitat was used in proportion to its availability in winter and spring, a comparison of seasons showed a slight (but not significant) shift toward mature pine habitat in winter. A small mammal prey base study indicated that in winter, relatively more small mammals occurred in this habitat compared to young pine, deciduous woods or oldfield habitat. Possibly then, a greater availability of this primary winter food source (part II) within mature pine habitat influenced habitat selection by gray foxes in this direction.

Similarly, significantly higher nocturnal use of young pine habitat in summer-fall months by gray foxes may have been partially due to the abundance of blackberries and other seasonally ripe fox foods present in this habitat type. Oldfield habitat also appeared to be selected (although not significantly) for in summer-fall months; this habitat type also contained an abundance of blackberries and other summer-fall fox foods. Deciduous forest was used approximately in proportion to its availability year-round; since it was the predominant habitat type on the ORR, covering an average of 47% of gray fox home range areas, high utilization occurred "incidentally". Deciduous woods contained a relatively high small mammal population (Figure IV-3) (important fox food in winter); although not quantified, this habitat type also

contained an abundance of other seasonally important fox foods, including squaw root (an important spring and early summer food), persimmon and cherry trees (important summer-fall foods), and probably an abundance of insects, including 17 year locusts in May, 1987. Factors other than the location of foods could also affect nocturnal habitat utilization.

High variation in habitat utilization among individual gray foxes within home ranges of similar landscape suggested that this area was sufficiently productive to leave "room" for individual habitat preferences. While changes in home range size did not appear to correspond to seasons (part III), seasonal shifts in habitat use did appear to correspond somewhat to location of seasonally available foods. This suggests that an adequate year-round resource base was contained within individual home ranges.

LITERATURE CITED

- Boyle, K.A. 1986. A comparison of methods of home range analysis. M.S. thesis, Clemson Univ. 67pp.
- Cairns, A.L., and E.S. Telfer. 1980. Habitat use by four sympatric ungulates in boreal mixed wood forests. *J. Wildl. Manage.* 46:849-857.
- Deuser, R.D., H.H. Shugart, and J.C. Randolph. 1976. Structural niches in a forest floor small mammal community. ORNL/TM-5004. 118pp.
- Don, B.A.C., and K. Rennolls. 1985. A home range model incorporating biological attraction points. *J. Anim. Ecol.* 52:69-81.
- Dunn, J.E. 1977. Optimal sampling in radio telemetry studies of home range. Univ. of Arkansas Statistics Lab. Tech. Rep. No. 5.
- Dunaway, P.B., and S.V. Kaye. 1961. Studies of small-mammal populations on radioactive white oak lake bed. *Trans. 26th North Amer. Wildl. and Nat. Res. Conf.*, Mar. 6-8:167-185.
- Follmann, E.H. 1973. Comparative ecology and behavior of red and gray foxes. PhD thesis, Southern Illinois Univ., Carbondale. 152pp.
- Fritzell, E.K., and K.J. Haroldson. 1982. *Urocyon cinereoargenteus*. *Mammal. Sp.* 189:1-8.
- Fuller, T.K. 1978. Variable home-range sizes of female gray foxes. *J. Mammal.* 59:446-449.
- Grinnell, J., J. Dixon, and J.M. Linsdale. 1937. Fur-bearing mammals of California. Vol. II. Univ. California Press, Berkeley. Pages 377-777.
- Hall, E.R. 1981. The mammals of North America. Vol. II. John Wiley and Sons, N.Y. Pages 601-1175.
- Hallberg, D.L., and G.R. Trapp. 1984. Gray fox temporal and spatial activity in a riparian agricultural zone in California's central valley. Pages 920-928 in Warner, R.E., and K.M. Hendrix, eds. *California riparian systems: ecology, conservation and productive management*. University of California Press, Berkeley.
- Haroldson, K.J., and E.K. Fritzell. 1984. Home ranges, activity, and habitat use by gray foxes in an oak-hickory forest. *J. Wildl. Manage.* 48:222-227.
- Heezen, K.L., and J.R. Tester. 1967. Evaluation of radio-tracking by triangulation with special reference to deer movements. *J. Wildl. Manage.* 31:124-141.

- Johnson, W.C., R.K. Schreiber, and R.L. Burgess. 1979. Diversity of small mammals in a powerline right-of-way and adjacent forest in east Tennessee. *Am. Midl. Nat.* 101:231-235.
- Kitchings, J.T., and D.J. Levy. 1981. Habitat patterns in a small mammal community. *J. Mammal.* 62:814-820.
- Layne, J.N. 1958. Reproductive characteristics of the gray fox in southern Illinois. *J. Wildl. Manage.* 22:157-163.
- MacDonald, D.W. 1980. Resource dispersion and the social organization of the red fox (*Vulpes vulpes*). Pages 918-949 in Chapman, J.A., and D. Pursley, eds. *Worldwide furbearer conf. proc.* Vol. II.
- , 1983. The ecology of carnivore social behavior. *Nature* 301:1743-1753.
- Mosby, H.S. 1971. Reconnaissance mapping and map use. Pages 119-134 in Giles, R.H., Jr., ed. *Wildlife management techniques.* The Wildlife Society by Edwards Brothers, Inc., Ann Arbor, Michigan.
- Nicholson, W.S. 1982. An ecological study of the gray fox in east central Alabama. M.S. thesis. Mississippi State University. 93pp.
- Nowak, R.M., and J.L. Paradiso. 1983. *Walker's mammals of the world.* Vol. I. 4th ed. The Johns Hopkins Univ. Press. 1362pp.
- Richards, S.H., and R.L. Hine. 1953. Wisconsin fox populations. Wisconsin Conserv. Dept. Tech. Wildl. Bull. 6. 78pp.
- SAS Institute Inc. 1985. *SAS user's guide: statistics.* Version 5 ed. Cary, N.C: SAS Inst. Inc. 956pp.
- Scott, T.G. 1955. Dietary patterns of red and gray foxes. *Ecology* 36:366-367.
- Seagle, S.W., H.H. Shugart, and D.C. West. 1984. Habitat availability and animal community characteristics. ORNL/TM-8864. 46pp.
- Sheldon, W.G. 1949. Reproductive behavior of foxes in New York State. *J. Mammal.* 30:236-246.
- Smith, G.J., J.R. Cary, and O.J. Rongstad. 1981. Sampling strategies for radio-tracking coyotes. *Wildl. Soc. Bull.* 9:88-93.
- Smith, T.R. 1976. An evaluation of vertically stratified traps for censusing small mammal populations. M.S. thesis, Univ. of Tennessee. 80pp.
- Springer, J.T. 1979. Some sources of bias and sampling error in radio-triangulation. *J. Wildl. Manage.* 43:926-935.

Steel, R.G.D., and J.H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. McGraw-Hill Book Co., New York. 633pp.

Sullivan, E.G. 1956. Gray fox reproduction, denning, range and weights in Alabama. J. Mammal. 37:346-351.

Sunquist, M.W. 1981. The social organization of tigers (Panthera tigris). Smithsonian Contrib. to Zool. No. 336. 98pp.

Trapp, G.R. 1978. Comparative behavioral ecology of the ringtail (Bassaricus astutus) and gray fox (Urocyon cinereoargenteus) in southwestern Utah. Carnivore 1:3-32.

Trapp, G.R., and D.L. Hallberg. 1975. Ecology of the gray fox. Pages 164-178 in M.W. Fox, ed. The wild canids. Van Nostrand Reinhold Co., N.Y.

Wood, J.E. 1958. Age structure and productivity of a gray fox population. J. Mammal. 39:74-86.

Wood, J.E., D.E. Davis, and E.V. Komarek. 1958. The distribution of fox populations in relation to vegetation in southern Georgia. Ecology 30:160-162.

Wooding, J.B. 1984. Coyote food habits and the spatial relationship of coyotes and foxes in Mississippi and Alabama. M.S. thesis, Miss. State Univ. 43pp.

Yearsley, E.F., and D.E. Samuel. 1980. Use of reclaimed surface mines by foxes in West Virginia. J. Wildl. Manage. 44:729-734.

Yoho, N.S., and V.G. Henry. 1972. Foods of the gray fox (Urocyon cinereoargenteus) on European wild hog (Sus scrofa) range in east Tennessee. J. Tennessee Acad. Sci. 47:77-79.

PART V

SUMMARY AND DISCUSSION

Gray fox (*Urocyon cinereoargenteus*) ecology was studied on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987. Objectives were to determine food habits, seasonal home range sizes, activity patterns and habitat utilization, and interrelationships among these factors. Scat analysis determined that foxes (like many other canids) may "switch" dietary trophic levels, consuming primarily animal prey in winter months, insect prey in spring (although this may have been an exceptional year due to the emergence of 17-year locusts), and fruit in summer and fall. Such major shifts were probably dictated by seasonal food availability, and revealed the catholicity in diet of gray foxes.

Home range sizes were determined from radio-telemetry data on a seasonal and annual basis. Mean composite home range size for 5 male and 5 female foxes was 3.97 km² (4.41 km² for 6 adults, and 3.32 km² for 4 subadults). ANOVA detected no significant differences in home range sizes among seasons based on dietary trophic level, food "abundance" and "scarcity" or breeding, pup-rearing and prebreeding. Changes in home range size between seasons for individual foxes was evident, but variability was high, and changes did not correspond with any obvious pattern. Territoriality and monogamy were suggested by closely coinciding home ranges of adult male-female pairs with little overlap between adult males or females. Heavy overlap of

subadult foxes (female in this case) with one adult male indicated that family aggregations may occupy the same home range. "Core areas", or areas of heavy use within home ranges remained relatively constant between seasons. Minimum gray fox density was estimated at 0.45 adults per km², although this may be considerably higher when "family aggregations", or subadults are accounted for.

Gray foxes were found to be most active nocturnally (66.6% active), inactive diurnally (21.9% active), and less active during early morning hours (26.6% active) than evening (54.3%). Chi-square tests comparing activity patterns for 4 different sets of months based on food type exploitation, relative food abundance, breeding cycle and degree of vegetative cover showed the most highly significant difference between months where vegetative cover (foliage) was high (May-October), when early morning and daylight activity levels were higher, than in months where cover was low (November-April).

Based on activity patterns, it was inferred that daytime habitat use was primarily for resting purposes, while nighttime utilization was primarily for travelling and foraging. A prey base study indicated (although not statistically significant) that winter relative small mammal abundance was highest in the mature pine habitat type. Habitat-utilization analysis determined that diurnally, gray foxes used young pine plantations with dense undergrowth more than expected relative to availability year-round. Excellent concealment value provided by such dense vegetation probably rendered this excellent resting habitat. Nocturnally, however, foxes used young pine, mature pine, deciduous forest and oldfield habitat approximately equally in proportion to

their availability in winter (although a slight shift toward mature pine was observed) and spring, but used young pine significantly more than expected in summer and fall. This may be attributed to seasonal changes in the location of available foods, with high concentrations of blackberries (Rubus sp.) in the young pine, and other fruits in the abundant deciduous forest habitat.

"Territory" is defined as a relatively fixed and exclusive area, presumably containing important resources, defended by an individual or group from intruders by aggression or advertisement such as scent marking or vocalizations (Kaufmann 1983; Brown and Orians 1970). A "home range" is simply the area in which an individual lives (Brown and Orians 1970; Burt 1943), and is not defined on the basis of specific behaviors, nor the exclusion of other individuals (Brown and Orians 1970). Since territoriality may be viewed as resource defense, a prerequisite then, is defensibility. Since time and energy costs of territorial defense may be high (Davies 1978; Kaufmann 1983) advantages conferred must be great. Overlapping home ranges may be more common then, where resources are abundant, while territorial behavior corresponds somewhat to scarcity of defensible resources (Jonkel and Cowan 1971; MacDonald 1980, 1983).

Advantages of territoriality may include exclusive access to food resources and the "certainty" conferred in familiarity with location and quantity of those resources (Davies 1978; Kaufmann 1983). This, in turn, may improve chances for survival and reproductive success (e.g. Lack 1966; Brown 1975; Messier and Barrette 1981). Other advantages

may include access to mates, shelter, distance from intraspecies-communicated disease and parasites, or other factors (Brown and Orians 1970).

A positive relationship between resource dispersion and home range (or territory) size has been suggested. This relationship has been reported for several carnivores, with home range areas expanding with decreases in prey availability or lower habitat productivity (e.g. Fuller 1978; Ward and Krebs 1985; Litvaitis et al. 1986; Nicholson 1982; Richards and Hine 1953). Others have reported that territory sizes remained constant, but contained a sufficient food supply for periods of food scarcity, or fluctuations in food supply (MacDonald 1980, 1983; Hersteinsson and MacDonald 1982; Kruuk and Parish 1982; Brand et al. 1976; Messier and Barrette 1981). Hence, these territory sizes also may have been influenced by resource dispersion.

The positive relationship between dietary trophic level and home range size (minus the effects of body size and metabolic needs) has often been associated with the relative differences in resource abundance and dispersion between primary (greater productivity) and secondary (lower productivity) trophic levels (e.g. McNab 1963; Schoener 1968; Gittleman and Harvey 1982; Harestad and Bunnell 1979; Mace et al. 1983). This study provided the opportunity to test this relationship within a single species, the gray fox, which exhibited the dietary habits of frugivore, insectivore, and carnivore, according to seasonal availability of foods.

It has been suggested that territoriality may not be necessary for survival or reproductive success (fitness) where resources are abundant

(Davies 1978; Ewer 1973; Kaufmann 1983; Jonkel and Cowan 1971). In geographical regions of seasonally scarce resources (winter), territoriality may be an important strategy to better insure individual fitness in the "worst case scenario". In the present study, resources may be seasonally abundant (summer and fall fruits), but also seasonally scarce (winter animal prey).

Although home range size was not constant for individual foxes among seasons in the present study, it appeared that adult foxes recognized the boundaries of neighboring fox's "composite" home ranges year-round, which therefore remained relatively exclusive for pairs or family aggregations (Figures III-1 to III-3). Although territorial defense could not be established in the current study, scats were often observed in prominent locations, such as along roads and at road intersections, often in piles of 2 or 3. This may have been indicative of "defense" by scent-marking, and has also been observed in several other studies on gray foxes (e.g. Trapp 1978; Richards and Hine 1953; Grinnell et al. 1937; Wood et al. 1958).

Due to small sample size and high individual variability, all conclusions are tentative, and subject to further examination. It appears that environmental factors (food availability) may have influenced the establishment of territories, within which were contained sufficient resources for periods of food scarcity (in this case winter), as well as periods of plenty. Seasonal changes in home range areas which are observed to correspond to changes in dietary trophic level were therefore not necessary to obtain sufficient resources. Seasonal shifts in habitat utilization, or area-utilization

within a territory could accomplish the goal of "finding enough food to survive".

The question of what influences home range or territory size was not conclusively determined in the present study. Nonetheless, some general rules are hypothesized. If, due to time and energy costs, animals defend only the minimum area required to provide adequate resources (in this case food) (Mace et al. 1983), the upper limit of gray fox home range size in east Tennessee may be determined by winter food availability, when presumably (animal) prey is dispersed more widely than spring, summer and fall food sources (insects and fruit). Although no significant differences in home range (territory) size were observed among seasons of frugivorous, insectivorous, or carnivorous food habits, the catholicity of gray fox food habits may enable the species to have relatively smaller territory sizes than similar-sized carnivores with diets of a higher flesh-content. A relatively low density, however, may have "permitted" larger territories than an area saturated with gray foxes. Yet, lean winters with relatively sparser prey density may have in turn limited the gray fox population. It has been suggested (MacDonald 1983) that periods of food scarcity may ultimately determine territory sizes. While the period of food scarcity corresponds to winter in east Tennessee, when foxes must rely on animal foods, it is further suggested that within a given area, the primary and ultimate determinant of territory size may be the highest trophic level on which a given species relies for any length of time, and only secondarily on the dispersion of those resources.

Future investigations might address the following issues:

- (1) Are gray foxes territorial? Investigation might be accomplished by a combination of radio-telemetry, observation and radio-isotope tags to distinguish scats of individual foxes, their time and location of deposit; (2) Does territoriality occur only where resources are scarce and/or defendable? Investigation might be accomplished by controlled experiments, or a comparison of studies between regions of differing habitat productivity, and of temporally constant versus temporally inconstant food production. Attention must be paid to large sample sizes, due to variability between individual gray foxes; (3) Do territory (or home range) sizes vary with habitat productivity? Investigation might be accomplished with the above methods.

LITERATURE CITED

- Brand, C.J., L.B. Keith, and C.A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. *J. Wildl. Manage.* 40:416-428.
- , 1975. The evolution of behaviour. W.W. Norton, New York. 761pp.
- , and G.H. Orians. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* 1:239-62.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24:346-352.
- Davies, N.B. 1978. Ecological questions about territorial behavior. Pages 317-350 in Krebs, J.R., and N.B. Davies, eds. *Behavioural ecology: an evolutionary approach*. Blackwell Scientific Publications, Oxford.
- Ewer, R.F. 1973. The carnivores. Comstock Publishing Assoc., Cornell Univ. Press, Ithaca, N.Y. 494pp.
- Fuller, T.K. 1978. Variable home-range sizes of female gray foxes. *J. Mammal.* 59:446-449.
- Gittleman, J.L., and P.H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.* 10:57-63.
- Grinnell, J., J. Dixon, and J.M. Linsdale. 1937. Fur-bearing mammals of California. Vol. II. Univ. of California Press, Berkeley. Pages 377-777.
- Harestad, A.S. and F.L. Bunnell. 1979. Home range and body weight - a reevaluation. *Ecology* 60:389-402.
- Hersteinsson, P., and D.W. MacDonald. 1982. Some comparisons between red and arctic foxes, Vulpes vulpes and Alopex lagopus, as revealed by radio-tracking. *Symp. Zool. Soc. Lond.* 49:259-289.
- Jonkel, C.J. and Cowan, I. McT. 1971. The black bear in the spruce pine forest. *Wildl. Monogr.* 27:5-57.
- Kaufmann, J.H. 1983. On the definitions and functions of dominance and territoriality. *Biol. Rev.* 58:1-20. 1983.
- Kruuk, H., and T. Parish. 1982. Factors affecting population density, group size and territory size of the European badger (Meles meles). *J. Zool. Lond.* 196:31-39.

- Lack, D. 1966. Population studies of birds. Oxford University Press, Cambridge. 341pp.
- Litvaitis, J.A., J.A. Sherbourne, and J.A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. J. Wildl. Manage. 50:110-117.
- MacDonald, D.W. 1980. Resource dispersion and the social organization of the red fox (Vulpes vulpes). Pages 918-949 in Chapman, J.A., and D. Pursley, eds. Worldwide furbearer conf. proc., Vol. II.
- . 1983. The ecology of carnivore social behavior. Nature 301:379-384.
- Mace, G.M., P.H. Harvey, and T.H. Clutton-Brock. 1983. Vertebrate home-range size and energetic requirements. Pages 32-53 in Swingland, I.R., and P.J. Greenwood, eds. The ecology of animal movement. Clarendon Press, Oxford.
- McNab, B.K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 97:133-140.
- Messier, F., and C. Barrette. 1981. The social system of the coyote (Canis latrans) in a forested habitat. Can. J. Zool. 60:1743-1753.
- Nicholson, W.S. 1982. An ecological study of the gray fox in east central Alabama. M.S. thesis, Univ. of Georgia. 106pp.
- Richards, S.H., and R.L. Hine. 1953. Wisconsin fox populations. Wisconsin Conserv. Dept. Tech. Wildl. Bull. 6. 78pp.
- Schoener, T.W. Sizes of feeding territories among birds. Ecology 49:123-142.
- Ward, R.M.P., and C.J. Krebs. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. Can. J. Zool. 63:2817-2824.
- Wood, J.E., D.E. Davis, and E.V. Komarek. 1958. The distribution of fox populations in relation to vegetation in southern Georgia. Ecology 39:160-162.

APPENDIX

Table A-1. Percent frequency, number, and percent dry weight of food categories and food items, on an annual basis, with taxa "nested" in preceding category or class, found in 170 fox scats on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

Food Items	% Total Weight	Number of Times Occurring	% Frequency
ANGIOSPERMAE	78.58	227	133.53
Persimmon (<i>Diospyros virginiana</i>)	43.43	71	41.76
Cherry (<i>Prunus serotina</i>)	20.18	22	12.94
Blackberry (<i>Rubus</i> sp.)	3.96	18	10.59
Squaw-root (<i>Conopholis americana</i>)	6.32	8	4.71
Wild grape (<i>Vitis</i> sp.)	0.26	6	3.53
Mulberry (<i>Morus</i> sp.)	1.95	5	2.94
Acorn (<i>Quercus</i> sp.)	0.07	5	2.94
Carolina buckthorn (<i>Rhamnus caroliniana</i>)	0.11	5	2.94
Dogwood berry (<i>Cornus florida</i>)	0.11	3	1.76
Virginia creeper (<i>Parthenocissus quinquefolia</i>)	0.35	2	1.18
Muscadine grape (<i>Vitis rotundifolia</i>)	0.08	2	1.18
Pokeberry (<i>Phytolacca americana</i>)	0.02	2	1.18
Redbud (<i>Cercis canadensis</i>)	0.01	2	1.18
Maple (<i>Acer</i> sp.)	Trace	2	1.18
Autumn olive (<i>Eleagnus</i> sp.)	0.02	1	0.59
Legume family (<i>Leguminosae</i> sp.)	0.06	1	0.59
Composite family (<i>Compositae</i> sp.)	0.01	1	0.59
Silky dogwood (<i>Cornus amomum</i>)	Trace	1	0.59

Table A-1 (continued).

Food Items	% Total Weight	Number of Times Occurring	% Frequency
Gum (<i>Nyssa</i> sp.)	0.03	1	0.59
Poison ivy (<i>Rhus radicans</i>)	0.02	1	0.59
Plum (<i>Prunus americana</i>)	0.09	1	0.59
Hickory (<i>Carya</i> sp.)	0.01	1	0.59
Pear (<i>Pyrus</i> sp.)	0.01	1	0.59
Grass (Unknown sp.)	0.94	42	24.70
Unidentified sp.	0.54	23	13.51
INVERTEBRATA	13.00	243	142.94
Beetle (Coleoptera)			57.64
Grasshopper (Orthoptera)			42.35
Locust (Homoptera)			18.82
Beetle larvae (Coleopteran larvae)			7.06
Ant (Hymenoptera)			3.53
True bugs (Hemiptera)			2.35
Cocoon (Lepidoptera)			1.18
Caterpillar (Lepidoptera)			1.18
Worm (Annelida)			1.18
Mayfly (Ephemeroptera)			1.76
Millepede (Diplopoda)			0.59
Centipede (Copopoda)			0.59
Pillbug (Isopoda)			0.59
Snail (Gastropoda)			1.18
Unidentified			2.94

Table A-1 (continued).

Food Items	% Total Weight	Number of Times Occurring	% Frequency
VERTEBRATA	8.42	78	45.87
MAMMALIA (MAMMALS)	7.58	48	28.53
Rabbit (Sylvilagus floridanus)	4.03	12	7.06
White-tailed deer (Odocoileus virginianus)	1.71	8	4.70
White-footed mouse (Peromyscus sp.)	0.18	6	3.53
Pine vole (Microtis pinetorium)	0.43	5	2.94
Woodchuck (Marmota monax)	0.79	3	1.76
Chipmunk (Tamias striatus)	0.13	2	1.18
Cotton rat (Sigmodon hispidus)	Trace	1	0.59
Skunk (Mephitis mephitis)	Trace	1	0.59
Bat (Lasiurus sp.)	0.01	1	0.59
Bat (Myotis sp.)	0.03	1	0.59
Short-tailed shrew (Blarina brevicauda)	Trace	1	0.59
Unknown small rodent (Rodentia sp.)	0.17	3	1.76
Unknown small mammal (Mammalia sp.)	0.10	4	2.35
AVES	0.38	10	5.88
Unknown sp.	0.38	10	5.88
AMPHIBIA			
Salamander (Plethodontidae sp.)	0.17	3	1.76
Leopard frog (Rana utricularia)	0.15	1	0.59

Table A-1 (continued).

<u>Food Items</u>	<u>% Total Weight</u>	<u>Number of Times Occurring</u>	<u>% Frequency</u>
VERTEBRATA (continued)			
OSTEICHTHYES	0.01	2	1.18
Bass	0.01	1	0.59
(Micropterus sp.)			
Unknown sp.	Trace	1	0.59
REPTILIA	0.13	1	0.59
Snake	0.13	1	0.59
(Colubridae)			
UNKNOWN VERTEBRATA	0.15	14	8.23
TOTAL	100.00	548	322.34

Table A-2. Winter (January-April), spring (May), and summer-fall (June-December) comparison of percent frequency and percent dry weight of food categories and food items, with taxa "nested" in preceding category or class, found in 170 fox scats on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

Food Items	Winter (n=42)		Spring (n=16)		Summer-Fall (n=112)	
	% Wt	% Freq	% Wt	% Freq	% Wt	% Freq
ANGIOSPERMAE	14.43	(92.86)	1.81	(43.75)	93.93	(161.61)
Persimmon (Diospyros virginiana)	3.02	(9.52)			52.00	(59.82)
Cherry (Prunus serotina)					24.32	(19.64)
Blackberry (Rubus sp.)					4.77	(16.07)
Squaw-root (Conopholis americana)			0.03	(6.25)	7.62	(6.25)
Wild grape (Vitis sp.)			1.08	(4.76)	0.19	(3.57)
Mulberry (Morus sp.)					2.35	(4.46)
Acorn (Quercus sp.)	0.75	(11.90)				
Carolina buckthorn (Rhamnus caroliniana)	0.32	(7.14)			0.10	(1.79)
Dogwood berry (Cornus florida)	1.19	(7.14)				
Virginia creeper (Parthenocissus quinquefolia)					0.42	(1.79)

Table A-2 (continued).

Food Items	Winter (n=42)		Spring (n=16)		Summer-Fall (n=112)	
	% Wt	% Freq	% Wt	% Freq	% Wt	% Freq
ANGIOSPERMAE (continued)						
Muscadine grape (<i>Vitis rotundifolia</i>)					0.10	(1.79)
Pokeberry (<i>Phytolacca americana</i>)					0.02	(1.79)
Redbud (<i>Cercis canadensis</i>)	0.11	(4.76)				
Maple (<i>Acer</i> sp.)			0.03	(6.25)	Trace	(0.89)
Russian olive (<i>Eleagnus</i> sp.)	0.21	(2.38)				
Legume family (Leguminosae)					0.07	(0.89)
Composite family (Compositae)	0.11	(2.38)				
Silky dogwood (<i>Cornus amomum</i>)					Trace	(0.89)
Gum (<i>Nyssa</i> sp.)	0.32	(2.38)				
Poison ivy (<i>Rhus radicans</i>)					0.02	(0.89)
Plum (<i>Prunus americana</i>)					0.11	(0.89)
Hickory (<i>Carya</i> sp.)	0.11	(2.38)				
Pear (<i>Pyrus</i> sp.)					0.01	(0.89)

Table A-2 (continued).

Food Items	Winter (n=42)		Spring (n=16)		Summer-Fall (n=112)	
	% Wt	% Freq	% Wt	% Freq	% Wt	% Freq
ANGIOSPERMAE (continued)						
Grass	2.48	(26.19)	1.74	(25.00)	0.69	(24.11)
(Unknown sp.)						
Unidentified	4.73	(11.93)	0.01	(6.25)	0.14	(15.19)
INVERTEBRATA						
Beetle	18.54	(107.14)	96.13	(275.00)	4.61	(137.50)
(Coleoptera)						
Grasshopper		(50.00)		(93.75)		(55.36)
(Orthoptera)		(9.52)		(75.00)		(50.00)
Locust		(7.14)		(100.00)		(11.61)
(Homoptera)						
Beetle larvae		(19.05)		(6.25)		(2.68)
(Coleopteran larvae)						
Ant		(2.38)				(4.46)
(Hymenoptera)						
True bugs		(11.90)				
(Hemiptera)						
Cocoon						(0.89)
(Lepidoptera)						
Caterpillar						(1.79)
(Lepidoptera)						
Worm						(1.79)
(Annelida)						
Ephemeroptera						(1.79)
(Mayflies)		(2.38)				

Table A-2 (continued).

Food Items	Winter (n=42)		Spring (n=16)		Summer-Fall (n=112)	
	% Wt	% Freq	% Wt	% Freq	% Wt	% Freq
INVERTEBRATA (continued)						
Millipede (Diplopoda sp.)						(0.89)
Centipede (Copopoda)						(0.89)
Pillbug (Isopoda)						(0.89)
Snail (Gastropoda)						(1.78)
Unidentified		(4.77)				(2.68)
VERTEBRATA	67.03	(100.00)	2.06	(18.75)	2.46	(29.46)
MAMMALIA	61.73	(73.81)	0.24	(6.25)	2.21	(14.28)
Rabbit (Sylvilagus floridanus)	32.03	(11.90)			1.27	(6.26)
White-tailed deer (Odocoileus virginianus)	11.42	(16.67)			0.79	(0.89)
White-footed mouse (Peromyscus sp.)	1.96	(11.90)			Trace	(0.89)
Pine vole (Microtus pinetorum)	4.63	(7.15)			Trace	(1.79)
Woodchuck (Marmota monax)	8.47	(7.15)				

Table A-2 (continued).

Food Items	Winter (n=42)		Spring (n=16)		Summer-Fall (n=112)	
	% Wt	% Freq	% Wt	% Freq	% Wt	% Freq
VERTEBRATA (continued)						
MAMMALIA (continued)						
Chipmunk (Tamias striatus)			0.24	(6.25)	0.13	(0.89)
Cotton rat (Sigmodon hispidus)					Trace	(0.89)
Skunk (Mephitis mephitis)	Trace	(2.38)				
Bat (Lasiurus sp.)					0.02	(0.89)
Bat (Myotis sp.)	0.31	(2.38)				
Short-tailed shrew (Blarina brevicauda)					Trace	(0.89)
Unknown small rodent (Rodentia sp.)	1.82	(4.76)			Trace	(0.89)
Unknown small mammal (Mammalia sp.)	1.09	(9.52)				
AVES						
	3.56	(11.90)			0.06	(4.46)
Unknown sp.	3.56	(11.90)			0.06	(4.46)

Table A-2 (continued).

Food Items	Winter (n=42)		Spring (n=16)		Summer-Fall (n=112)	
	% Wt	% Freq	% Wt	% Freq	% Wt	% Freq
VERTEBRATA (continued)						
AMPHIBIA						
Salamander (Plethodontidae sp.)	1.74	(4.76)			0.01	(0.89)
Leopard frog (Rana utricularia)	0.10	(2.38)			0.01	(0.89)
	1.64	(2.38)				
OSTEICHTHYES						
Bass (Micropterus sp.)	Trace	(2.38)			0.01	(0.89)
Unknown sp.	Trace	(2.38)			0.01	(0.89)
REPTILIA						
Snake (Colubridae)			1.72	(6.25)		
			1.72	(6.25)		
UNKNOWN VERTEBRATA						
	Trace	(7.15)	0.10	(6.25)	0.17	(8.94)
TOTAL	100.00	(300.00)	100.00	(337.50)	100.00	(328.57)

Table A-3. Physical measurements of the gray foxes captured on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

ID Sex/Age	Weight (kg)	Front Pad Lgth (cm)	Hind Pad Lgth (cm)	Pes (cm)	Tail Lgth (cm)	Total Lgth (cm)	Girth (cm)	Neck (cm)	Ear Lgth (cm)	Date Trapped
62 F/S	3.9	3.3	3.8	12.2	31.1	60.0	27.5	16.9	6.3	10/01/86
63 F/S	3.9	3.0	3.9	13.1	33.9	60.5	34.0	16.9	6.0	02/25/87
64 F/S	2.7	3.8	3.7	12.8	33.0	61.0	25.5	17.7	9.4	09/26/86
66 F/S	2.6	3.4	4.1	11.4	29.7	66.5	24.3	16.0	5.7	09/25/86
74 F/A	3.5	3.9	4.0	12.2	26.0	53.5	28.0	17.9	8.6	09/14/86
78 F/S	2.9	3.6	4.0	12.2	29.0	54.0	26.8	17.0	8.1	09/19/86
80 F/A	2.8	3.6	3.8	12.1	24.3	55.5	28.0	17.4	7.1	09/09/86
-- F/S	2.3	3.6	4.4	11.2	31.0	55.0	24.6	14.4	8.7	09/08/86
58 M/A	3.5	3.6	3.2	12.1	---	70.0	32.6	18.5	6.5	03/16/87
65 M/A	3.0	3.5	4.3	12.8	33.0	57.5	26.0	17.0	7.3	06/13/87
69 M/A	4.0	3.8	4.1	13.5	32.1	61.7	31.0	18.8	5.3	09/25/86
76 M/A	3.6	4.0	4.0	13.3	33.0	60.0	30.5	18.3	7.6	09/14/86
82 M/A	3.9	4.2	3.6	13.1	35.0	60.0	28.5	18.0	6.9	09/07/86
84 M/A	3.6	4.3	3.5	---	36.0	56.7	---	19.2	6.0	09/11/86

Table A-4. Composite minimum convex polygon home range estimates for 5 male and 7 female gray foxes radio-tracked September 1986-August 1987, Oak Ridge Reservation, east Tennessee.

ID	Sex	Age	Number of Locations	Period Radio- Tracked	Number of Days Tracked	Composite Home Range (km ²)
58	M	A	25	03/16/87-08/31/87	4	6.91
69	M	A	231	09/25/86-06/09/87	35	3.25
76	M	A	248	09/14/86-08/31/87	37	4.36
82	M	A	293	09/07/86-08/31/87	39	4.01
84	M	A	130	09/11/86-03/02/87	20	2.83
62	F	S	102	10/01/86-01/12/87	17	2.09
63*	F	S	119	02/25/87-08/31/87	21	17.94
64	F	S	236	09/26/86-05/12/87	37	3.08
66	F	S	271	09/25/86-08/31/87	44	2.09
74	F	A	266	09/14/86-08/31/87	42	5.08
78	F	S	308	09/19/86-08/31/87	48	5.54
80*	F	A	18	09/09/86-11/03/86	4	1.24

Home range parameters:

$$\bar{X}_{\text{male}} = 4.27 \text{ km}^2$$

$$\bar{X}_{\text{female}} = 3.67 \text{ km}^2$$

$$\bar{X}_{\text{adult}} = 4.41$$

$$\bar{X}_{\text{subadult}} = 3.32$$

$$\bar{X}_{\text{total}} = 3.97 \text{ km}^2$$

*Home range not included in calculations.

Table A-5. Minimum convex polygon home range estimates for breeding, pup-rearing, and prebreeding seasons for 5 male and 7 female gray foxes radio-tracked September 1986-August 1987, Oak Ridge Reservation, east Tennessee.

ID	Sex	Age	Breeding (Jan.-Mar.)	Pup-rearing (Apr.-July)	Prebreeding (Aug.-Dec.)
58**	M	A	---- (10)	----- (15)	-----
69	M	A	2.39 (69)	1.52 (41)	2.36 (121)
76	M	A	2.91 (80)	4.02 (80)	3.08 (88)
82	M	A	2.85 (84)	2.82 (81)	3.23 (128)
84*	M	A	2.53 (53)	-----	1.71 (77)
62*	F	S	-----	---- (5)	2.09 (97)
63**	F	S	7.72 (28)	14.81 (60)	7.37 (31)
64	F	S	2.63 (89)	1.02 (38)	1.86 (109)
66	F	S	1.92 (85)	0.82 (85)	1.57 (101)
74	F	A	3.57 (94)	2.61 (71)	4.16 (101)
78	F	S	2.95 (86)	3.46 (85)	5.37 (137)
80**	F	A	-----	-----	1.24 (18)

$\bar{X}_{\text{male}}$ 2.67 (286) 2.79 (202) 2.60 (414)

$\bar{X}_{\text{female}}$ 2.77 (354) 1.98 (279) 3.01 (545)

$\bar{X}_{\text{total}}$ 2.72 (640) 2.32 (481) 2.83 (959)

*Mean home range size for season inserted in calculations to prevent omission of all data for animal in ANOVA procedure

**Not included in calculations

Table A-6. Minimum convex polygon home range estimates for "abundant" and "scarce" food seasons for 5 male and 7 female gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

ID	Sex	Age	Abundant (May-Dec.)	Scarce (Jan.-Apr.)
58*	M	A	----	6.91 (25)
69	M	A	2.35 (137)	2.72 (94)
76	M	A	3.68 (140)	3.45 (108)
82	M	A	3.46 (179)	3.16 (114)
84	M	A	1.71 (77)	2.53 (53)
62*	F	S	2.09 (97)	---- (5)
63**	F	S	14.77 (73)	13.38 (46)
64	F	S	2.08 (116)	2.59 (120)
66	F	S	1.62 (155)	2.20 (116)
74	F	A	4.52 (148)	4.30 (118)
78	F	S	4.75 (191)	3.02 (117)
80**	F	A	1.24 (18)	----
$\bar{X}_{\text{male}}$			2.80 (53)	3.75 (394)
$\bar{X}_{\text{female}}$			3.01 (707)	3.03 (471)
$\bar{X}_{\text{total}}$			2.92 (865)	3.43 (1240)

*Mean home range size for season inserted in calculations to prevent omission of all data for animal in ANOVA procedure

**Not included in calculations

Table A-7. Total small mammal captures and recaptures (in parentheses) in 4 habitat types over 4 seasons, September 1986-August 1987 on the Oak Ridge Reservation, east Tennessee.

Habitat Type	Grid ID	Season				Habitat Totals
		Fall	Winter	Spring	Summer	
Young pine	A	3(0)	3(0)	15(2)	8(7)	
	B	2(0)	4(4)	7(9)	7(4)	49(26)
Deciduous forest	A	4(1)	5(2)	9(10)	10(15)	
	B	4(3)	8(5)	21(21)	13(21)	74(78)
Oldfield	A	3(3)	9(6)	1(0)	7(10)	
	B	6(0)	8(5)	9(10)	6(2)	49(36)
Mature pine	A	2(1)	8(3)	16(17)	4(6)	
	B	1(2)	22(8)	9(10)	7(9)	69(56)
Season totals		25(10)	67(33)	87(79)	65(74)	241(196)

Table A-8. Relative abundance and species composition (recaptures in parentheses) of small mammals between 4 habitat types on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

Species	Habitat Type				Total
	Young Pine	Deciduous Forest	Oldfield	Mature Pine	
<u>Blarina brevicauda</u>	7(0)	----	5(0)	2(2)	14(20)
<u>Cryptotis parva</u>	4(0)	----	2(0)	----	6(0)
<u>Glaucomys volans</u>	----	----	----	1(0)	1(0)
<u>Mus musculus</u>	----	----	2(3)	1(0)	3(3)
<u>Ochrotomys nuttalli</u>	19(14)	4(5)	1(2)	----	24(21)
<u>Peromyscus</u> sp.	12(10)	69(73)	24(20)	64(54)	169(157)
<u>Reithrodontomys humulis</u>	7(2)	----	12(9)	----	19(11)
<u>Sigmodon hispidus</u>	1(10)	----	3(0)	----	1(0)
<u>Tamias striatus</u>	----	----	----	1(0)	1(0)
TOTALS	50(26)	73(78)	49(34)	69(56)	241(196)

Table A-9. Characteristics of gray fox daytime resting sites and dens on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

Cover Description	Den Description	Number of Foxes
Dense, brushy brambly vegetation in a powerline or phoneline.	-----	4
In mixed hardwood forest, adjacent to phoneline as described above.	"Cave" in rocky ledge.	2
In mixed hardwood forest.	(1) Hole tunnelled into ground.	2
	(2) Abandoned woodchuck den, 2 entrances, adjacent to gully.	
Behind office buildings adjacent to a steep bank with deciduous forest and phoneline.	-----	1
Clearcut area with brushy vegetation, adjacent to stream.	Under heavy brush in ditch bank (possibly in a hole).	2
Mixed pine-hardwood with slash on forest floor.	-----	2
Deciduous woods with clean understory.	Hole under roots of windthrown hardwood.	2
Young pine plantation with dense, brambly vegetation.	-----	2

MONTHS (SEPT. 1986 - AUG. 1987)													
ID SEX/AGE	9	10	11	12	1	2	3	4	5	6	7	8	TOT. n
58 M/A													25
65 M/A													--
69 M/A													231
76 M/A													248
82 M/A													293
84 M/A													130
62 F/S													102
63 F/S													119
64 F/S													236
66 F/S													271
74 F/A													266
78 F/S													308
80 F/A													18
TOT. n	41	260	164	304	229	244	210	233	149	174	141	98	2247

KEY
 T = TRAP RELATED INJURY
 V = KILLED BY VEHICLE
 P = APPARENT PREDATION
 F = TRANSMITTER FAILURE
 N = DEATH FROM APPARENT NATURAL CAUSES

Figure A-1. Duration of radio-tracking, number of locations, and fate for 13 gray foxes on the Oak Ridge Reservation, east Tennessee, September 1986-August 1987.

VITA

Katie was born in Washington, DC in 1959. She received a Bachelor of Arts degree in Philosophy from the George Washington University in 1982. After returning to school for an academic background in the sciences at North Carolina State University, Raleigh, she entered the University of Tennessee Graduate Program in Ecology in September 1985. She received her Master of Science degree in Ecology in June 1988.